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#### THE

## ANATOMY & PHYSIOLOGY

OF THE



## LOW-FLY

(Musca vomitoria Linn,)

## A MONOGRAPH

BY

BENJAMIN THOMPSON LOWNE, M.R.C.S. Eng.

ILLUSTRATED WITH TEN PLATES.

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## PREFACE.

In submitting the following pages to the scientific world, although I do so knowing their many shortcomings, I trust there is sufficient that is new to make amends for any slight inaccuracies, which could, perhaps, hardly have been avoided, since so little has been done to pave the way for the present investigation.

The Plates, which form no inconsiderable feature in this Work, have been carefully executed on copper, by myself; and I have spared no trouble to make them as perfect as possible.

I have endeavored to give prior authorities for my statements as often as possible, except when the facts are well known, but much work upon the anatomy of insects is so scattered that it has often not been in my power to discern whether I am entitled to priority of discovery.

#### PREFACE.

I have divided the text into two parts, in order that the more general facts may be separated from the more special; and I have further had the most technical portions of the subject printed in smaller type. The correct appreciation of homologies has been my aim throughout the entire work, and the whole has been drawn up from my own dissections. I have made no statements merely upon the authority of others, except in one or two instances, in which this is specially stated.

Dr. Weismann's elaborate researches on the Development of the Diptera have greatly aided me; and my best thanks are due to Mr. C. Stewart, of St. Thomas's Hospital, for the kind manner in which he has allowed me access to his cabinet, and the readiness with which he has always aided me by his opinion or advice.

I have to acknowledge also the kindness of Mr. Curties for the aid he has afforded me in bringing out the present Work.

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## INTRODUCTORY NOTE ON THE HOMOLOGIES OF INSECTS.

In the following pages, I am aware, that in describing the antennal and optic segments as posterior to those composing the mouth, I have done some violence to the ordinarily received views of many distinguished naturalists; but I think the sequence of the cephalic segments in the fly is too plain to be easily misconstrued.

Professor Huxley,\* states that he believes the upper surface of the head in insects is sternal instead of dorsal, and he founds this belief on the apparent curvature of the embryo; but I think it possible that the extraordinary development of the lateral parts of segments behind the mouth, arching over and surrounding the mouth segments, may give rise to the appearance of curvature.

My knowledge of the Crnstacea is too limited to allow me to give a positive opinion, as to which segment is most anterior in them, but I see no reason why the optic and the antennal segments should not be dorsal plates of segments posterior to the mouth, largely developed and arching over it, whilst the corresponding ventral plates are either wanting or amalgamated with the ventral portions of other segments. Such a supposition appears to me to be as likely to be correct as that their dorsal plates are absent, whilst the ventral plates occupy the dorsal region, and unite by their anterior border (made posterior by their flexion) with the anterior edge of a dorsal, plate belonging to another segment.

As the names I have given to the various plates, forming the head of the fly, depend upon their relations with each other, and are mainly borne out by the distinctness of the four plates in each segment, and the manner in which they articulate with each

\* The agamic reproduction of Aphis, Linn. Soc. trans. vol. xxii,

#### NOTE ON THE HOMOLOGIES OF INSECTS.

other; as well as by the fact that the ganglia of the mouth segments (myœsophageal and oral ganglia) are anterior to the ganglia of the eyes and antennæ: and that the optic and antennal segments are developed from imaginal discs, contiguous with those of the thorax. I give them for what they are worth and must leave those, who know the homologies of the arthropoda generally better than I do, to judge whether the facts are sufficient to justify my conclusions. It is true Dr. Weismann has named certain lobes, which he has found in the embryo larva, behind the antennal and optic segments, maxillary and mandibular segments; but I do not think any connection can be traced between these lobes and the organs of the mouth. I confess, however, I have never been able to distinguish them.

With regard to the thorax if any substantial homology can be traced between it and any of the segments of the Crustacca, I should be inclined to look upon it as the homologue of the middle-body\* of the latter from its late development in the fly, and from its bearing the ambulatory legs.

I have stated, inadvertently in a note, on page 3, that "seventeen segments is the number assigned on theoretical grounds to all true insects" but no sufficiently stable theory has, pehaps, been formed to justify the expression : and I find, according to Gerstäcker, that the Orthopterahave eleven abdominal segments, forming an exception to the number I have given.

I find I agree with M. Duthiers, in describing the opening of the sexual organs between the eighth and ninth abdominal segments, but did not see the great importance of the observation at the time I made it. Lastly, strangely enongh, I have made use of an expression in the second paragraph on page 7 which is identical with one used by Sir John Lubbock† in his paper on the development of Ephemera, although I did not know at the time, that it had been previously used.

+ Linn. Soc. trans, vol. xxv. page 489.

<sup>\* 1</sup> use this term as it is used by F. Muller in his "Facts for Darwin" translated by Dallas.

## PART I.

#### GENERAL OBSERVATIONS ON THE ANATOMY AND PHYSIOLOGY OF THE FLY.

#### Section I.—Introductory Remarks.

THE type, or plan, upon which insects are organised is so very different from the type of the vertebrata, that if we wish to understand the Anatomy of the Fly, it is necessary to bear in mind the chief characteristics of the class to which

#### DESCRIPTION OF PLATE I .- FRONTISPIECE.

This plate represents a dorsal view of the whole of the internal organs as they appear in situ, when the integument of the back is removed, except on the right side of the thorax, where the great dorsal muscles have also been removed to show the deep layers. Commencing at the head, the following organs are displayed: the frontal sac occupies the frontal region and is tinted yellow: on each side of this sac are the antennal nerves, and the sides of the head are occupied by the great eyes, which are seen in section : between these the cephalic nerve centre with its main tracheal trunks occupies the greater part of the head ; it is cut through horizontally near the eyes to exhibit the arrangement of the deep tracheze. The left side of the thorax is occupied by a mass of muscles, longitudinal near the centre, and vertical at the side; the central muscles are more especially used to depress the wings in flight, and the lateral are partly elevators of the wings and partly flexors and extensors of the legs being inserted into their basal joints. The tracheal vessel, which occupies the posterior portion of this side is connected with the posterior thoracic spiracle. On the right side, the chyle stomach and convoluted salivary gland occupy the portion nearest the mesial line. Immediately external to the latter is the main lateral trachea collapsed, except its posterior portion which remains filled with air ; it communicates with the posterior thoracic spiracle. The nerve to the halter is seen crossing this portion of the tracheal trunk. The anterior tracheal vessel exhibited on this side is

it belongs, and to investigate its relations to other insects, not only in its perfect state, but in its various stages of development.

Insects are articulate animals, organisms in which the external integuments fulfil the same purposes in the economy as the osseous skeleton does in the vertebrata; and, just as the typical structure of the latter is most fully exemplified in the skeleton, so the integumental system in the articulata affords the most obvious indications of the type upon which they are organised.

In the lowest members of this great division of the Animal kingdom we find the body composed of a series of rings or *Annuli*, united to each other by a membrane, each ring having a separate nerve centre, and being similar to every other ring in the body of the animal, except the first, which is modified so as to form a distinct head very low in the scale of life.

As we ascend, we find organs of sense developed upon the anterior rings, however, still in a very rudimentary form; an alimentary canal traverses the whole series, and a decided concentration of the nervous system takes place about its anterior extremity. If we add to these characters the presence of a mouth furnished with a pair of hooks, which not only serve the purpose of teeth, but also assist the animal materially in locomotion, and are in fact, one of three pair of modified limbs which

from the anterior spiracle; it passes forward into the head and communicates behind with the lateral trachea. Two small pulmonary sacs are also seen communicating in front with this trunk. The muscles of the deep layer are probably all more or less concerned in flight. The abdomen is occupied in the mesial line by the dorsal vessel, on each side of which are the large abdominal pulmonary sacs; behind these the convoluted bile tubes are colored red. The salivary glands may be seen crossing the pulmonary sacs. The sides of the abdomen are filled with the mature ovaries, and its apex is occupied by the rectum and rectal papille.

#### INTRODUCTORY REMARKS.

exist in the mouths of insects,\* we shall have an idea of the larva of the fly, commonly known as the gentle or maggot : which, although it resembles one of the lowest of the articulata, except in the nervous system, as will be seen afterwards possesses the power of development into one of the highest of its forms.

The integumental system of this larva consists of seventeen segments, † of which the three anterior alone have lost more or less of their original annular form. These, both in the larva and perfect insect, compose the mouth, and in both are provided with three pair of modified limbs, although the existence of the first pair is less certain in the larva, owing to the very rudimentary

\* Each segment in the lowest articulate is normally furnished with two pairs of lateral appendages or rudimentary limbs, one pair placed above the other, the superior being dorsal and the inferior ventral; at least, such is their arrangement in annelides. Both pairs are much modified in the higher forms, and are often entirely suppressed.

The segments themselves may be said to consist typically of four plates, a ventral, a dorsal, and a lateral plate on each side ; the superior appendages being placed between the lateral and dorsal, and the inferior between the lateral and ventral plates. In insects the wings, when they exist, represent the dorsal appendages, being placed between the superior and lateral plates. It seems to me probable that the spiracles and their tracheæ are likewise lateral appendages. If such be the case, I think it quite likely, from the number of lateral appendages, that more than three segments really exist in the thorax, especially as the anterior thoracic spiracles are placed between two segments and the four posterior legs occupy a similar position; so that possibly these may be latera' appendages of undeveloped segments. This is certainly the case if the spiracles with their tracheæ are homologues of lateral appendages, like the wings and legs. This appears to me not unlikely from their position. and further from the consideration that the lateral appendages of many annelides are both respiratory and motor organs, ( M. Quatrefages Hist Nat. des Annelès Nouv. Suites a Buffon, Tom. i. p. 19). And we must remember the tracheæ of insects are merely modified processes of the skin developed inwards instead of outwards.

+ This is the typical number assigned on theoretical grounds to all true insects, which always have the body in the perfect state divided into three parts, the head, thorax and abdomen. The head consists of five

condition of this segment, and the extreme modification it undergoes in the development of the perfect insect. The fourth and fifth segments are united above in the larva as well as in the perfect form, and each bear a pair of sense organs; the antennæ and the eves. The sixth segment of the larva bears the anterior spiracles or breathing pores; but, together with the next two, the seventh and eighth, and in fact all the succeeding ones, is unprovided with legs. These three segments correspond to the thorax of the perfect insect, which is however not only provided with six legs, but also with a pair of wings, appendages of the seventh segment. The eighth or last thoracic segment is likewise usually supplied with wings in insects, but in the Diptera, the class to which the fly belongs, they are suppressed and their place is occupied by a pair of small organs, called halteres or balancers. Of the remaining nine segments which form the abdomen of the perfect insect, four are modified and converted into the hard parts of the sexual organs, which are more or less internal.

Although the segments of the larva and perfect insect correspond exactly in the manner above indicated, nevertheless the head and thorax of the fly, from the fourth to the eighth segment inclusive, are not developed from the corresponding larval segments.

It may be here observed that the histological elements, that is, the elementary tissues of the perfect fly, cells, fibres, &c.,

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segments, or according to some, of six, making eighteen in the whole body; but as the segments of the head of the fly, both in the larva and perfect insect are very distinct, I am inclined to the former view. The thorax constantly bears three pairs of legs and consists of three distinct segments; unless, as may appear probable from the position of the legs and spiracles, the thorax has six, when the whole number of segments in the insect would amount to twenty, the number found in the highest scolopendrize (*Scutigera. Lam.*), where the head consists of five segments, and the body of fifteen, which each bear a pair of legs, but are united above, so that only eight appear on the dorsum,

#### INTRODUCTORY REMARKS.

differ in no important character from those of the highest animals. The chief difference is seen in the larger size of the gland cells. The muscular fibres are described as larger than in vertebrates. This has probably arisen from the larva and not the perfect insect, having been examined. All the tissues in the larva, except the nerve cells and fibres, are four or five times as large as in the perfect insect, but this seems to depend rather upon rapidity of growth than upon any inherent difference.

The striated muscular fibre in the fly varies from 1-3000th of an inch in diameter in the muscles of the halteres and abdomen, to 1-1000th in the pharyngeal muscles and those of the legs, but in the larva several of the muscles have fibres as large as 1-200th of an inch in diameter.

All the muscular fibres of the alimentary canal and dorsal vessel exhibit striæ. The only non-striated muscles I have been able to detect are the great longitudinal dorsal muscles of the thorax; these consist of long clear fibres less than 1-5000th of an inch in diameter, swollen at intervals and containing nuclei. Numerous slightly granular cells lie amongst them. No myolemma exists, although the tracheal vessels appear to separate them into bundles; so that they are soft and easily broken up into a mass of cells and fibres.

Nuclei exist permanently in the myolemma of the striated muscles, and appear in rows when they are treated with acetic acid. In many the fibres branch, and the branches are as large as the primitive fibres. The muscles of the abdomen and crop are flat bands of fibres with well marked striæ; those of the crop terminate in pointed and often in branched extremities. The muscles are either inserted into the integument directly or through the medium of apodèmes, a clear transparent tendinous structure intervening, which appears to be continuous with the myolemma. The whole muscular tissue is firm, but pale.

The gland cells of the salivary tubes are 1-1000th of an inch in diameter; those of the rectal papillæ are 1-500th of an inch in diameter; the conical epithelium of the stomach has a long diameter of 1-1500th of an inch. The liver cells are polygonal, filled with pigment and oil globules, with a diameter of about 1-1500th of an inch : all have well marked nuclei. Adipose tissue does not exist, but large quantities of fat are laid up in the folliculate glands and liver cells, especially in the former.

Nerve cells vary from 1-5000th to 1-2500th of an inch in diameter; they are irregular in form, often being branched. The nerve fibres vary very much in size; those of the muscles branch, and end in loops; others,

especially in the organs of special sense, end in nerve cells. The nerves of the ganglia of the head and thorax are rounded, the fibres of which they consist being enclosed in a neurilemma; but those of the sympathetic system appear to have no neurilemma : they spread out into flattened branched expansions, and have numerous branching nerve cells scattered amongst them.

#### Section II.—Development.

Perhaps the most startling difference between the vertebrate and the articulate divisions of the animal kingdom is seen in the manner of their development. In insects, as in many other articulata, this takes place by a process termed Metamorphosis, the creature not only being entirely and suddenly changed in appearance, but also in habits of life. Usually there are three periods in the existence of an insect, the first characterised by rapid growth and a comparatively small exercise of animal functions, the second by a period of apparent quiescence, during which growth is changed into development, and lastly one in which the animal functions are seen in their highest perfection; these are called respectively the larval, pupal, and imaginal states.

In the larval state, where growth is rapid, the hard integument is usually shed periodically, its place being supplied by new layers deposited beneath it, just as the cuticle in vertebrates is renewed by younger epithelial cells, or as the old bark of trees is replaced by younger layers. The larva of the fly forms an exception and does not shed its skin. After the full growth is attained, the insect commonly assumes a different form, called a pupa or chrysalis when it becomes inactive, and a nymph when a greater or less amount of activity remains. In a certain number of days the pupa case bursts, or the nymph sheds its skin, and the perfect insect emerges, partially developed at first, but in a few minutes or hours, as the case may be, assuming its new functions

#### DEVELOPMENT.

and form in their greatest perfection. Growth and development now cease as far as the individual is concerned, to give place to the generative function.

Every degree of metamorphosis exists amongst insects, from that in which the larva, nymph, and imago, closely resemble each other, where the successive changes are merely those of ordinary development, as in the cockroach, to that in which the change is so complete that it might almost be doubted whether the larva and imago should be considered the same individual at all, so closely does the process resemble an alternation of generation. This is the case in the fly.

Dr. Weismann, in Germany, as long ago as 1865\* pointed out that the development of the fly differs remarkably from that of most insects, in an elaborate memoir upon the subject; and two years after, in another upon the development of a species of gnat, Corethra plumicornis, proposed the division of insects into two classes, according to the presence or absence of certain structures in the larva which he calls Imaginal discs. † This distinguished naturalist asserted in his former paper, that the head and thorax of the fly does not depend for its development upon the corresponding larval segments, but that these parts are developed from a series of discs (Imaginal discs) firmly adherent to the nerves and tracheæ of the anterior extremity of the larva; and he goes on to add, "I believe in all those insects in which the anterior larval segments are unprovided with appendages (legs) the head and thorax of the Imago are entirely redeveloped, whilst in those in which the larva is furnished with legs, these parts depend for their formation upon the anterior larval segments."

Startling as the assertions of that writer appear, I have been fortunate enough to confirm them myself, and not only to confirm

\* Kolliker and Siebold Zeitschrift, band xiv-xvi. † Imaginal Scheiben.

them, but I think to add to them as regards the development of the proboscis. I believe that those segments of the fly immediately connected with the functions of vegetative life, those surrounding the anterior portion of the alimentary canal,—that is, the proboscis,—as well as the abdominal segments, are immediately dependent upon the corresponding larval segments for their development and form; whilst the head and thorax with all their appendages, the chief centres of animal life, are developed from Weismann's Imaginal discs, which do not coalesce with each other until the third day of the pupa state, so that these replace the larval segments from the fourth to the eighth inclusive.

The brain seems to form a centre around which these changes take place; even this organ is entirely altered, but by a process similar to ordinary development. The other structures are formed at the expense of a granular fluid which is chiefly derived from the so-called fatty bodies; these extend along the entire length of the larva on either side of the alimentary canal.

The skin of the larva of the fly is not shed when it reaches maturity, but dies and becomes very hard, turning yellow at the first, then red, and afterwards almost black. It forms the pupa case. This is not the representative of the skin of the pupa in most insects, for the corresponding larval skin is usually shed, and the pupa case is either altogether wanting, as in many hawk-moths and butterflies, or it is replaced by a cocoon of silk spun by the larva, as in the silk moth, or by some other adventitious covering.

The respiratory function ceases, and all the organs proper to the maggot undergo degeneration soon after the formation of the pupa case. The nerve centres grow rapidly, and the Imaginal discs unfold into delicate cellular expansions, which coalesce with each other, and with the new layers of cells formed within the three anterior and nine posterior larval segments, and ultimately form an exceedingly delicate membrane corresponding to the pupa skin of butterflies. In both, this marks out the position

#### THE INTEGUMENT.

of the new organs about to be developed, and in both, this is shed when the insect emerges from the pupa. These changes complete what Dr. Weismann calls the first stage of the development of the fly—the formation of the pupa.

It may be confidently asserted that not one structure exists in the fly as it exists in the maggot. Every portion of the larva, except the brain, and perhaps the basement membrane of the alimentary canal, undergoes rapid degeneration, and the fly is formed within the pupa skin by a process of redevelopment.

#### Section III.—The Integument.

The integumental system of the perfect fly originates upon the inner surface of the pupa skin, but as its parts become fully developed they shrink away from the pupa skin, so that it forms a loose investing membrane around the new formed fly, and may be looked upon as one of the integuments shed in the process of development; for, although it is never thickened and indurated in the fly, it is precisely analogous to the pupa case in the lepidoptera, which is always more or less hardened. The reason of its not being hardened in the fly seems to be due to the fact that it is invested in the pupa shell or last larval integument.

The integuments of insects are usually said to consist of three layers, and these may be easily traced in the fly. The outermost is transparent and continuous over the whole surface of the insect, investing all the appendages and processes of the skin, even the hairs, and covering the surface of the eyes. It appears to be continuous with the lining membrane of the tracheal system, and to extend throughout the digestive cavity, although it is somewhat modified in the latter. a

This layer is usually called the cuticle or epidermis, but the term is unfortunate as it is quite unlike the cuticle in vertebrates, or, indeed, any structure found in them; it is persistent and not deciduous. The cells from which it is formed appear early in the development of the insect and ccalesce into an apparently structureless membrane of extreme toughness, which has the remarkable property of being quite insoluble in a hot solution of caustic potash; I shall, therefore, substitute the term protoderm for this layer.

The continuity of the protoderm is a fact well worth consideration at the commencement of the study of the anatomy of insects, as the terms insect, articulata, and articulate animal, are extremely liable to mislead, and to induce one to believe that the various segments are distinct and separable. Such is not really the case, but certain portions of the protoderm are thickened by the induration of the epithelial cells beneath it, which become inseparably united to it and to each other, and so produce the hard parts of the integument.

The two layers beneath the protoderm consist of epithelial cells in various stages of development; these are best observed in those parts of the integument which are transparent, as in the lips of the proboscis, and between the different plates of the pectus. The more superficial layer in these parts in the young fly will be found to consist of a single layer of flattened angular cells, containing well marked nuclei and beautifully coloured with bright orange-coloured pigment. These cells are about 1-1000th of an inch in diameter, and have a great tendency to adhere at their edges. In the adult fly they form a continuous membrane, but their nuclei become apparent on the addition of a little acetic acid. I shall call this layer the mesoderm.

Beneath this, numerous spheroidal nucleated cells, slightly angular by mutual pressure, are disposed in a layer of several cells in thickness; they seldom contain pigment, and correspond closely to the rete-mucosum or deep layers of the cuticle in ver-

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#### THE INTEGUMENT.

tebrates, but differ in being largely supplied with nerve filaments, which ramify in a branching network amongst them. Following the nomenclature I have already commenced, I think endoderm an appropriate name for this innermost cuticular layer.

The development of the mesoderm and endoderm is usually in an inverse ratio, and this is no more than we might expect, seeing that they are really different states of the same tissue. In the fully developed fly the cellular structure of the mesoderm is almost or entirely lost, but it can be demonstrated in many cases by carefully macerating the integument, drying it, and mounting it in balsam,—especially when viewed by the aid of the polariscope. Its cellular structure is, however, beautifully apparent in the insect soon after it emerges from the pupa. The whole coloration, as well as the hardness of the integument, is due to the indurated mesoderm. As has been already observed it can only be separated from the protoderm in those parts of the insect in which it is but slightly developed.

The pigment with which the hard parts of the mesoderm are chiefly coloured in the fly is deep blue or violet : whatever its chemical nature may be, the colour depends upon oxidization. It is first to be met with in the fat bodies of the larva. These are perfectly white, but when cut from the larva and exposed to the air they rapidly assume an inky blackness; and the same is true of the molecular fluid with which the pupa skin is filled. When the perfect insect emerges from the pupa and respiration again commences, the integument is nearly white, or a faint ashy colour prevails. This soon gives place to the characteristic blue or violet tint, first immediately around those portions most largely supplied with air vessels, but soon over all those parts of the insect which assume this colour; light seems to have little to do with the process, but it is more rapid in warm than in cold weather. The fat bodies of the larva are not permeated by air vessels, which will account for their retaining their whiteness. The pigment is finely granular when examined by high powers.

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The chemical composition of the indurated mesoderm is but partially understood. It is commonly said to be composed of chitine, from its resemblance to a coat of mail. The induration is partly due to animal tissue and partly to deposits of earthy salts, especially phosphate of lime, which form beautiful double refracting crystals in the wing cases of many beetles.\* The animal tissue is unlike the horny matter of vertebrates in being insoluble in a hot solution of caustic potash, thus resembling vegetable cellulose from which it is said to differ, however, in containing nitrogen.

The hairs with which certain parts of the body are clothed are developed from the three layers of the integument. The bulb is a single cell of the endoderm, and its cavity is continuous with the hollow cavity of the hair. The hair itself is composed of fibres which run through its entire length, giving it a channelled appearance when sufficiently transparent. These are probably developed from cells or nuclei of the mesoderm; whilst the whole is invested by the protoderm. The hairs in the pupa at the end of the first week consist only of hollow processes of the protoderm filled with very transparent cells or granules. No hairs are developed on the pupa skin.

The base of each hair is surrounded by a thickened ring; this is quite apparent from its earliest appearance, when the ring exists only as a fold of the protoderm.

<sup>\*</sup> I have used the term Crystal for these circular bodies, because I believe they are similar to those remarkable bodies which were first produced artificially by the late Mr. Rainey by the crystalization of salts in viscid fluids, and which are now known to abound in the animal kingdom. Some naturalists think these spots are only due to tension of the organic substance of the elytra, but Mr. Hislop, who has paid the subject much attention, tells me that their out-line is far more definite, when seen with polarized light, than that of any spots he has seen produced by tension alone, and that they disappear entirely when the wing-cases are treated with chlorine or strong acids, whilst the lines of tension, which are distinctly visible in the same elytra, are not effected by these reagents.

#### THE NERVOUS SYSTEM.

#### Section IV .- The Nervous System.

The nervous system, or rather, that part which is analogous to the cerebro-spinal system of vertebrates, is next to the integumentary in point of importance as far as regards type. Insects belong to that division of the animal kingdom which Professor Owen terms Homogangliata, that is, animals in which the nervous system is represented by a pair of nervous cords which traverse the ventral portion of the body, and lie next to the integument, uniting and forming a ganglion for each segment, from which the proper nerves of the segment are given off. No insect that has yet been examined departs from this type so much as the fly and its allies; for, even in the larva state, the whole of the nervous system is collected in the anterior segments, and the pair of ventral cords do not exist; whilst, in the imago, with the exception of two small ganglia in the proboscis, there are but two nerve centres, one situated in the head, and one in the thorax.

The first of these, called the cephalic ganglion on account of its position, is the homologue, that is, the anatomical representative of the œsophageal ganglion or ring of the lower forms of life; it surrounds the æsophagus and gives off four pairs and one single nerve, which are distributed to every part of the insect's head. It is connected with the great thoracic nerve centre by a thick cord which represents the double ventral cord, typical of the insecta.

The nerves given off from this ganglion, or more correctly speaking, collection of ganglia, for it is really composed of at least six, may be properly divided into two classes, those which consist entirely of nerve fibres having their origin in its substance, and those of which some of the nerve fibres at least, probably the greater portion, merely pass through it and have their real origin in the thoracic ganglion.

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The first class comprises five nerves,\* those of the great compound eyes and antennæ, and the single nerve which supplies the ocelli, or simple eyes.

The two remaining pairs of nerves are distributed to the proboscis. The larger supply the greater part of that organ, but chiefly the palpi and lips, and the smaller, which give off filaments to the two small ganglia already mentioned, are almost entirely lost in the muscles of the pharynx. Both pairs are probably motor-sensory, or compound nerves.

The cephalic ganglion is in fact the centre of the special senses in the fly. It is the analogue, that is the physiological equivalent of the ganglia at the base of the cerebrum in vertebrates; and if, as I firmly believe, the antennæ are organs of smell, it strictly represents the olfactory and optic lobes of fishes. Next to bees and ants, that of the blow-fly is the largest known in any insect proportionally to its size, being about thirty times larger than the cephalic ganglia of the larger beetles. But a more positive indication of a higher type of organization than even the relative bulk of the sensory ganglia is found in the fact that two very remarkable convoluted nerve centres connected by a commissure, each about 1-30th of an inch in diameter, surmount the cephalic ganglion, and are connected to it by a pair of distinct peduncles; these are extremely like the pedunculated convoluted nerve centres which occupy the same position in bees and ants, first described by M. Felix Dujardin, † and considered by him as analogous to the cerebral lobes of the higher animals. That naturalist failed to distinguish these organs

\* There is no nerve corresponding to the recurrent nerve of Lyonetfalsely called sympathetic by some authors, but a true sympathetic or organic nerve system exists in the fly.

<sup>†</sup> F. Dujardin sur le Système Nerveux des insectes, Ann. Sc. Nat. Serie III. Tom. xiv. 195. and "Quelques Observations sur les Abeilles" Ibid. xviii 231.

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in the fly, probably owing to their being imbedded in the substance of the cephalic ganglion. No one who has once seen them can doubt their far-advanced type above the ordinary ganglia of insects, and the superior intelligence manifested by the insects possessing them is not difficult to perceive. In fact, long before I detected these organs in the fly, I felt almost sure I should eventually find them, from the fact that many of the acts of this insect bear evidence of some memory at least; for instance, the manner in which flies will avoid a person who is pursuing them is clearly more than an ordinary reflex act.

Nevertheless, it must be conceded that most of the acts of insects are probably entirely reflex, or the result of impressions from without, and this coincides with the comparative bulk of the organs of sensation over that of the higher nerve centres.

M. Faivre, \* however, thinks otherwise, from the fact that in his experiments on the Dytiscus, that insect always gyrated to the left when the right side of the supra-œsophageal ganglion was removed, and to the right when the left was operated on, from which he argues the existence of voluntary power. He supposes the supra-œsophageal ganglion to be analogous to the brain of vertebrates; but M. Faivre clearly removed the great organs of sensation, and the rotatory direction pursued by the insect was probably entirely due to its seeking the direction in which the light proceeded, and so turning away from the injured side.

The thoracic ganglion gives off ten pairs of nerves, besides one single one distributed to the abdomen, and the great trunk which unites it to the cephalic ganglia. It is the homologue of the thoracic and abdominal ganglia of the typical homogangliata, and is, therefore, like the cephalic, a compound gan-

\* M. Faivre sur le Cerveau des Dytisques, Ann. Sc. Nat. Serie II. Tom viii. 245. glion. This is the nerve centre of animal life; its nerves are both motor and sensitive; it gives off likewise two pairs of nerves, which are supplied to organs of special sense; and its destruction results in the instantaneous death of the insect. If a pair of forceps are dexterously used so as to crush the whole thoracic ganglion at once, not a single movement will follow its destruction, except it be the slightest possible quivering of the muscles.

On the other hand, the removal of the insect's head, and with it of course, the whole cephalic ganglion, does not destroy the life of the trunk and limbs, but reflex movements can be produced for hours after by touching any part of the integument, but especially the integument of the abdomen.

When the head is removed from the fly there is nothing more striking than the different character of the phenomena exhibited by the parts. In the head a convulsive movement of the tongue and antennæ follows the division of the nervous cord which unites the two nerve centres ; this continues at most a few seconds, but no reflex act follows the application of external stimulus afterwards. Of course we cannot tell to what extent the functions of the cephalic ganglion remain, but their duration is probably short. Perhaps they cease as soon as the nerve of communication between the head and thorax is severed. On the other hand, although the trunk continues to manifest signs of life for many hours, no movements, except those which result from the stimulus or shock produced by dividing the great cephalo-thoracic nerve trunk at the moment of division, take place, except the respiratory movement of the abdomen, till some external stimulus is applied. A breath of air, or a touch with a needle point in any part of the integument, will produce vigorous movement of the legs and wings for hours after decapitation,-resulting either in an attempt to run or fly,and a little water or dust placed upon the posterior tarsi or

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These facts go far to prove that the same acts are always produced by external stimulus in the living fly, in other words, that they are reflex and not voluntary; they also show how extremely sensitive the integuments are to external impressions, and that their hardness does not prevent their being the seat of the sense of touch to a very great extent. Lastly, as there is nothing irregular in any of these acts after decapitation, it seems that the co-ordination of muscular movements is due to this nerve centre, a function, which, according to the experiments of M. Faivre,\* is performed by the sub-œsophageal ganglion in Dytiscus, and probably in all beetles : but I believe the homologue of this ganglion is transferred in the fly to the thoracic nerve centre, as the inferior portion of the posterior cephalic segment enters into the composition of the thorax, and not of the head. Thus the thoracic nerve centre appears to be the analogue of the cerebellum, medulla oblongata, and spinal cord of the vertebrata.

The nerves of the viscera are derived from a separate system of ganglia, and differ in structure from those of animal life, like the nerves of organic life, or the sympathetic system of vertebrates, to which they may be justly compared. The chief ganglion of this system is situated at the junction of the thorax and abdomen, but numerous smaller ganglia varying in size are scattered over the visceral organs, and the whole are connected by a complex system of minute nerves, which form a close network over all the viscera. Dr. Lockhart Clark tells me he has described a similar system of nerves in the earthworm.

Ann. Sc. Nat. IV. Tom viii 245.

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#### Section V .- The Wings and Legs.

The wings and legs are the most important thoracic appendages; their homologies have been already discussed.\*

The wings consist of a double layer of the protoderm, which may be demonstrated when the insect first emerges from the pupa, as the upper and under layers are then easily separated. The nervures are folds in one or both layers, which are strengthened by the development of epithelial cells in their interior. The larger ones contain the tracheal vessels and nerves, the latter being chiefly distributed to the bulbs of the hairs on the nervures. In the earlier stages of development the wings are represented by mere crumpled sacs attached to the lateral tracheæ of the larva; afterwards they become sacs of the protoderm on the sides of the thorax in the pupa.

Several complicated folds of integument project into the cavity of the thorax at the insertion of the wing, by which the muscles are attached which regulate its position, but the real muscles of flight are not connected with the wing at all. They consist of a longitudinal mass which fills the greater portion of the back, and the wings are so attached that the flank forms a kind of fulcrum upon which they are elevated or depressed by every alteration in the convexity of the back. The great longitudinal dorsal muscles, by shortening the thorax, increase its convexity and depress the wings, which are again elevated by the flattening of the back and lengthening of the thorax, due partly to its own elasticity and partly to the action of the lateral thoracic muscles, which are vertical in their direction. So that in point of fact the flight of insects is merely a modification of crawling, both being effected by the alternate approximation and extension of several segments. This may be confirmed by direct experiment;

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\* See Page 3,

#### THE WINGS AND LEGS.

for, by taking a recently killed fly and using a pair of dissecting forceps, placing one blade behind, and the other in front of the upper part of the thorax, the movements of flight may be produced by alternately compressing and relaxing the forceps; the wings should be extended in order that the full effect may be seen. The amount of alteration in the convexity of the back which is sufficient to depress the wings to their fullest extent, is so slight that it is scarcely perceptible to the eye.

It is a remarkable fact, and one worthy of special attention, that the great longitudinal theracic muscles exhibit no striæ, but consist of muscular fibres similar to those of organic life in the higher animals. This is an anomaly for which I can suggest no reason, unless it be the immense rapidity of the vibrations into which they throw the thoracic parietes.\*

The legs consist of four parts : the coxa or hip, composed of two pieces, which unites the limb to the thorax, the femur or thigh, the tibia or leg, and the tarsus or foot; the last three are tubular, and each articulation contains the muscles which move the succeeding one. The tarsus consists of five pieces, the first of which contains a pair of muscles, which move the second upon it. but the remaining four contain none; the last bears a pair of pads upon which the insect walks, and a pair of hooks above them. Both hooks and pads are connected with a single apodéme which projects into the last tarsal joint and is continued as a fine chitinous thread or tendon through the tarsus and tibia, and terminates in a bipenniform muscle which arises from the interior of the femur.

The foot pads are amongst the most interesting parts of the insect, because they enable it to walk upon smooth surfaces in an inverted position, apparently in defiance of the laws of gravity. Long ago

<sup>\*</sup> The description of the histological elements of these muscles is given at page 5.

this was first ascribed by Dr. Derham<sup>\*</sup> to the exhaustion of air from the foot pads; recently, it has been supposed to be due to the exhaustion of air from the extremities of the hairs with which the pad is clothed;<sup>†</sup> others have ascribed it to be the hold<sup>‡</sup> which these minute hairs take of trifling irregularities of surface, but none of these explanations are correct, and one of the earliest notions upon the subject is the nearest to the truth; that is, that the feet secrete a glutinous fluid which glues them to the surface on which the insect walks. When the pads are carefully examined it will be seen that they have no cup-shaped cavity beneath them, but that they are hollow with a nipple-like protuberance projecting into each. This will be seen more plainly by pressing upon the tarsus which forces it into the pad; by cutting off the end of the pad first, it may be exposed in this manner, and will be found to consist of a closed sac.

This sac fills the whole of the last four tarsal joints and is lined with pavement epithelium; it secretes a perfectly clear viscid fluid which exudes from it into the pad, and fills its cavity as well as the hollow hairs with which its under surface is covered. These hairs open by trumpet-shaped mouths, and the disc of each mouth is kept full of the fluid. Sometimes, when the insect is captured and held between the finger and thumb, it exudes so rapidly that the pads are soon covered with a little glistening drop of it, which may be collected upon a glass slide where it rapidly solidifies; it is insoluble in water and solidifies under that fluid. The whole contents of the tarsus becomes solid very rapidly as soon as the insect is dead, or the part is removed.

<sup>\*</sup> Kirby and Spence, Introduction to Entomology. The whole history of the various opinions of different Naturalists upon this subject are given at length.

<sup>&</sup>lt;sup>†</sup> J. Hepworth, Roy. Micros. Soc. Journal, vol. iii, 314. T. West. Linn Soc. Trans. vol. xxiii. 393.

<sup>‡</sup> Blackwall, Linn. Soc. Trans. vol. xvi, on the pulvilli of insects.

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There is no essential difference in the pads of flies and the pulvilli of beetles, moths, and other insects; the same fluid is secreted in all. The only difference is that the pads of flies are membranous and transparent, instead of hard and opaque.

The feet of the smaller house-fly are the best to show the manner in which the viscid fluid exudes from the extremities of the trumpet-shaped hairs, as they are very large in this species, and a glistening bead of fluid can be seen plainly at the extremity of each hair by placing the living insect under the microscope. The foot-prints left upon glass by flies consist of rows of dots corresponding to these hairs ;—this is best seen in those of the lesser house-fly from their greater size.

The whole appears precisely analogous to the manner in which caterpillars and spiders suspend themselves by silken threads. In both cases the fluid is exuded from minute pores and bears the weight of the insect, the only difference being in the nature and quantity of the fluid exuded. Much discussion has arisen as to the manner in which flies liberate their feet, and it has even been objected that they would become so firmly adherent after a time that the insect would be glued to the spot. Nothing can be simpler than the arrangement by which the foot is liberated, and in the healthy insect the secretion probably never becomes solid as long as it remains in contact with the foot. It is sufficiently glutinous, even in the fluid, or rather semi-fluid, state it assumes as it exudes, to sustain the weight of the insect, when the strain is put equally upon all the hairs, of which there are about 1200 on each pad; but when the pad is removed obliquely, so that each row is detached separately, the resistance amounts practically to nothing. A neat experiment will demonstrate this even to the most sceptical. If a piece of adhesive label be cut for convenience into a pear-shaped disc, an inch in diameter, and caused to adhere to the hand by slightly damping it, a force of many pounds applied to the narrow extremity in the axis of the paper will not stir it, whilst it is immediately removed, with very little resistance, when the force is applied so as to lift it gradually up.

The direction and length of the hairs upon the pad are so adapted to the oblique direction in which the strain is put upon them when the tarsus is straight, that the insect has a perfectly secure hold; this is immediately released as soon as the tarsus is curved, which is effected by the long slender tendon already mentioned. In the small house-fly the pads themselves are capable of being curved, for the tarsal tendon branches, and is inserted into the distal extremity of each pad.

The legs are developed from six pear-shaped corpuscles adherent to the nerves and tracheæ of the larva; the changes these undergo are seen in Plate VI., and are described in the second part of this work.

#### Section VI .- The Digestive System.

The viscera of the fly are remarkable for their symmetrical arrangment, a fact well worthy of note, as it is at variance with the usual disposition of the viscera of animals, although I believe lateral symmetry will prove the rule amongst insects.

The organs of the mouth are extremely modified so that they form a complicated proboscis admirably adapted for the purpose of collecting food by suction; and, although all the parts homologous to the six lancets of the gadflies so terrible in those insects, are present, they are all more or less intimately united to the sheath of the proboscis, so that they are quite incapable of inflicting a wound, but form by their union a long tubular mouth. The extremity of the organ bears a pair of large fleshy lobes, which form an oval sucker when open, by which the insect collects its food, either receiving the nutriment so collected at once into the opening of the mouth, which is placed between the lobes, or straining the fluid from the solid part of the material on which it is feeding by means of a set of channels (*false tracheæ*),

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#### THE CIRCULATION.

which open beneath by a very fine fissure and run from the margin to the centre of the lobes, and then open into the mouth. This is a provision highly necessary to the fly, as it feeds upon halfrotten pulpy substances, which would otherwise entirely fill its long tubular mouth and completely stop it up. A shuttleshaped chitinous organ supports the parts of the mouth, and is enclosed within the proboscis. This acts as a pump, drawing the fluid aliment from the mouth of the insect, and injecting it into the sucking stomach or crop.\*

The crop is a large reservoir for food, and is situated in the abdomen, it is capable of holding a sufficient supply of nourishment for several days. No solid food is taken by the fly, as it lives entirely upon fluids or such substances as are dissolved by its copious saliva, which is secreted by a pair of large tubular salivary glands. The aliment is gradually regurgitated from the crop into the proventriculus and chyle stomach,<sup>†</sup> which extends the whole length of the thorax, and which is lined with cylinder epithelium undistinguishable from that in the highest vertebrates.

The chyle stomach passes insensibly into the intestines, which are about one inch in length. A pair of large bile tubes open into them near their inferior extremity, and form a tubular liver of considerable magnitude by continually dividing, and end in blind extremities; they are very tortuous, and are filled with liver cells, containing fat globules and pigment.

#### Section VII.—The Circulation.

The circulation of the blood in insects is carried on without the aid of blood-vessels. The circulating fluid is contained

\* Sucken-Magen, Weismann, + Chylus-Magen, Ibid.

in the visceral cavity and bathes all the internal organs. A single vessel runs the whole length of the back, commencing near the apex of the abdomen and terminating in the head, called the dorsal vessel. It is open at either extremity, and serves the purpose of a heart pulsating rythmically, and pumping the circulating fluid from the posterior extremity of the insect, into the head, from which it returns amongst the viscera. The pulsation of this vessel may be observed in the fly just after the insect emerges from the pupa case, before its integuments become hardened and opaque; it makes about 180 pulsations in a minute.

The dorsal vessel being small in comparison to the cavity of the body, the return of the blood is necessarily slow. This gives rise to a peculiar distribution of the viscera as well as to a very important modification of the respiratory organs and function, adapting the insect to pass a life of great vital activity, with a comparatively slow circulation.

Thus the salivary glands not only extend the whole length of the thorax in complicated convolutions, but pass into the abdomen and only terminate at its posterior extremity. This brings them into relation with the blood throughout a large part of the circulation. So the ductless glands, called fat bodies or corps graisseux, which seem to be analogous to the ductless glands of animals, and to be concerned in the elaboration of the circulating fluid itself, are found largely developed in the abdomen, and also, though more sparingly, in the head. The analogues of the kidneys, the rectal papillæ, pulsating organs having a central cavity alternately filled and emptied of blood by a rhythmic muscular act, are placed near the posterior extremity of the dorsal vessel, so that they excrete the effete matter from the circulation just before the return of the blood to the head and thorax. The same may be said with regard to the disposition of the liver tubes, only to a less degree.

#### THE RESPIRATORY SYSTEM.

#### Section VIII .- The Respiratory System.

The chief modification of structure dependent upon the peculiarity of the circulation is in the respiratory organs, the air being carried to all the tissues in a system of tubes, called tracheæ, from their cavity being kept open by a spiral fibre, or more often by a series of rings which run into each other so as to appear spiral. These tubes open externally by pores called spiracles, and are merely an involution, so to speak, of the protoderm or external layer of the skin ; they ramify in the interior of the insect, dividing in an arborescent manner, until at last they attain the minute diameter of something like 100,000th of an inch, when they anastomoze freely with each other and form a network of tubules over the surface, and in the substance, of every organ.

The tracheal tubes consist of two coats. The internal, in the substance of which the spiral fibre is developed, corresponds to the protoderm, and like it, is formed from cells, which in the case of the perfect fly originate in the pupa case, in the earliest stages of the formation of the imago. Similar rings to those in the tracheæ are developed, either from cells or nuclei of the protoderm, in the false tracheæ of the proboscis, an important fact, as it is confirmatory of the view I have taken of their homologies.\* The external layer is easily detected before the fly attains its full development; it is thick and structureless at first, containing nuclei, and thickest in their vicinity; it seems to be a mere collection of protoplasm. As the

\* The origin of the rings of the false tracheæ is even better seen in the tongue of the Cricket, where the nuclear form is retained throughout life, near the edges of the organ; this was first pointed out to me by my friend, Mr. C. Stewart.

insect reaches maturity, this layer becomes extremely attenuated, and forms a structureless membrane very difficult to trace; it is best seen in the tracheæ of the larva.

The spiral fibre has been described as a distinct coat between the other coats, but it is really part of the internal. M. Blanchard\* even supposed that a circulation of the nutritive fluid takes place in insects, in a channel between the coils of the spiral and the two layers of membrane, which he supposed to be connected with the dorsal vessel; but no such channel exists.<sup>†</sup>

It is extremely difficult to say at what point in the division of the tracheal vessels the spiral disappears. Most of the vessels which are as small as the 10,000 th part of an inch, exhibit no trace of transverse marking, but a very distinct double contour is observable in their walls; whilst in others of the same magnitude distinct transverse markings are visible with high powers, at irregular intervals. The smallest divisions have probably no spiral, and consist, I believe, entirely of the external coat, which assumes the form of a structureless membrane.<sup>‡</sup>

The larger tracheæ of the head and thorax of the perfect fly differ very considerably in structure from those already described, and form large reservoirs of air. Numerous sacculi which lie between the muscles, mere dilatations of these tracheæ, open into them, and the main lateral tracheæ terminate in a pair of large sacs at the base of the abdomen, the pulmonary sacs of the French naturalists. The walls of these vessels and their sacculi are composed entirely of a brittle membrane, corresponding to the

#### \* Comp. Rend. xxiv.

 $\dagger$  It is needless to repeat the arguments against such a circulation, which even if the spiral were a distinct layer, are fully given in the xxviii. and xxix. vols. of the Comp. Rend.

<sup>‡</sup> In the stag beetle the irregularity of the spiral in the smaller tracheal tubes is easily seen.

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protoderm ; it is extremely delicate, covered with reticulated wrinkles, and marked with striæ, transverse to the wrinkles, not the 12,000th of an inch apart, which render it iridescent. This membrane, as well as the inner coat of the other tracheæ, assumes a smoky tint in the adult insect, probably from the oxidization of minute particles of pigment contained in its substance.\*

The spiracles or external openings are all protected, either by folds, the edges of which are armed with minute spiculæ, or by a ring of spiculæ formed of chitine, and the admission of air is controlled by a structure somewhat resembling a pair of callipers,—acted upon by a special muscle,—which surrounds the tracheæ and is connected with their internal coat.<sup>†</sup>

The manner in which the circulation of air in the tracheæ is carried on in insects is by no means certain ; that it is exceedingly vigorous in the fly may be fairly assumed from the rapidity with which the vapour of chloroform and other volatile substances act upon the insect; and from the fact that a little turpentine, applied with a camel's hair brush to one of the anterior thoracic spiracles, produces instantaneous insensibility. The great vital activity of the fly indicates that the respiratory function is very perfect; in bees again the high temperature of the hive tends to the same conclusion.

I believe the pressure of the thoracic muscles acting unequally upon the main membranous tracheæ and their sacculi, aided by the valves at the spiracles, is the chief agent by which the air is propelled through the smaller tubules. If such be the case, the ordinary muscular acts of the insect would be sufficient to keep up a very perfect circulation, as it is scarcely conceivable that any muscle can contract, without giving, rise to some movements of the air in the large tracheæ. When a fly is held by the wings

\* The disposition of the main tracheal vessels is shown in Plate I.

† Landois, Kolliker Zeichrift, Band. 17, 105.
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it will be observed to make vigorous exertions with all its legs at regular intervals, varying from sixteen to thirty or more in a minute. With each of these acts the valves of the anterior spiracles are closed for a short space of time, during which the air must necessarily be driven through the small these, proving that these are respiratory efforts. Their regularity and their being accompanied by a contraction and dilatation of the abdomen confirms this view. Again, if placed under the exhausted receiver of an air pump, and removed before death has taken place, the insect's abdomen immediately collapses more or less from the exhaustion of the tracheal vessels, and more especially of the abdominal pulmonary sacs; and the refilling of the tracheal system is accompanied by violent movements of the legs and wings.

Although, under ordinary circumstances, no proper respiratory movement of the abdomen can be observed, if the head be removed, a regular respiratory movement of the abdominial parietes may be seen, and the same is observable when the insect is at rest. There can be no doubt that every alteration in the capacity of that cavity acts directly upon the pulmonary sacs, and so upon the whole tracheal system. These abdominal movements are scarcely sufficient to account for the rapid change of air in the small tracheæ of the head and thorax, and are probably only accessory to the ordinary muscular movements in their effect on the air in the tracheæ. The change in the volume and shape of the thorax during the movements of the wings, although slight in itself, is probably from its great rapidity also an important respiratory agent; and lastly, the pressure of the muscles upon the smaller tracheæ undoubtedly assists the movement of air in these tubes by emptying them, the elasticity of their internal coat causing them to dilate and refill as soon as the pressure is removed.

The humming sound made by the insect seems to depend upon several causes, but the chief seems to be the rapid vibration of

### THE FAT BODIES AND DUCTLESS GLANDS.

the edges of the values of the thoracic trachem,\* perhaps also of a plate in the forehead, which covers a membranous cavity in that part. The sound is attended with a violent vibration of the whole thorax, probably chiefly produced by the rapid contraction of the dorsal muscles. The vibration of the wings may, and probably does, give rise to a peculiar note; but owing to their movement being always attended with vibrations of the thorax, it is difficult to determine how much is due to them. Another note is produced by the rubbing of the head against the thorax.<sup>†</sup>

#### Section IX.—The Fat Bodies and Ductless Glands.

Two dissimilar structures have been confounded under the term fat bodies, the omenta of the larva, and the ductless glands of the imago.

The former consist of plicated cellular expansions formed of large flat cells of hexagonal outline, adhering to each other by their edges, which are firmly attached to the lateral tracheæ of the larva, in which a store ef elaborated nutriment is laid up for the development of the pupa.

The fat bodies or ductless glands of the image consist of closed follicles, arranged upon the tracheæ in an arborescent manner; the follicles themselves are composed of structureless membrane, and contain peculiar nucleated corpuscles, nuclei, and granules; in the mature insect they are often loaded with oil globules. From

\* Dr. H. Landois, Die Ton und Stimmaparate der Insecten, Kolliker Zeitchrift, Band. 17, 105.

+ Dr. H. Landois and W. Thelen, Der Tracheenverschluss bei den Insecten. ibid. Band 17, 187.

the great similarity of the contents of these follicles to those of the spleen and other ductless glands in the vertebrata, I have not the slightest doubt as to the similarity of their functions, which is the elaboration of the circulating fluid.

## Section X .- The Organs of Special Sense.

The organs of special sensation in the fly are the compound and simple eyes, the antennæ, the halteres, and probably the frontal sac, the cephalo-sternum, the lobes of the proboscis, and maxillary palpi.

With the exception of the visual organs, which closely resemble the essential parts of those of the vertebrata, great difficulties occur in determining the functions of the sensory organs, and the removal of any of these, even when this can be done without injury to other parts, is no test of its function. Flies seem completely helpless when the antennæ are removed, and quite unable to fly if the halteres are cut off, yet this is no proof that the quickness of the insect is due to its antennæ, or that flight is a function of its halteres. All the senses seem so closely bound together, or correlated to each other in insects, that we can hardly expect any to be normally exercised when one is damaged. Even in man himself, we know that nothing but experience enables him to judge correctly of objects with a single sense, and we should hardly expect a dog to act normally, if one of its senses were suddenly removed. Apart from the pain which may accompany the removal of an organ, the new relations with the external world might be expected to produce an abnormal manifestation in a creature, almost all the acts of which are probably purely reflex. So that structure, analogy, and the habits of the insect, are really the only guides in such investigations.

The great compound eyes each consist of between four and five thousand facets; each facet being a circular biconvex lens, the thousandth of an inch in diameter, set in a flat hexagonal frame. Behind every facet is a transparent cone, surrounded by dark red pigment, which terminates posteriorly in a rod, connecting it, through the medium of a layer of nerve cells, with a clear distinct nerve filament.

The convexity of the facets of the cornea is a most important point, as the vision of insects has been supposed to derive its distinctness from the number of separate facets. It has been supposed that distinctness of vision is due in them to the absorption of all the rays of light which have not the same direction as the axes of the cones and rods of which the eye is composed. Such is not the case, however, in the fly; the lenticular structure of the cornea is most distinct, and the focus of each lens appears to correspond with the apex of the transparent cone beneath it. The necessity of any adaptive power to distances, it may be, is entirely obviated by the smallness of the lenses, as the rays of light emanating from a point an inch distant from the eye could not possibly make a greater angle than a minute, so that virtually all rays would be parallel when the distance of objects from the eye exceeded an inch. Yet it is far from certain that even adaptation to distance is not effected by a special arrangement of tracheal tubes between the rods and cones.\* Perhaps nearer objects are perceived only by the ocelli, which are specially adapted for near vision, for which the comparative flatness of the lenses of the compound eyes seems but little fitted.

The great convexity and extent of the compound eyes is such that it enables the insect to see all the objects in at least fourfifths of the sphere which surround it; but as no two facets look towards the same spot, no provision for stereoscopic vision exists in these organs, even if the insect be able to perceive near objects by them. These deficiencies seem to be supplied by the ocelli, which, from the great convexity of their refracting

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\* Page 88,

medium and their position in a triangle upon the forehead, seem not only eminently adapted for the perception of very near objects, but also for the nicest possible appreciation of their distances from the insect.

Beneath the cornea in the ocelli is a thick layer of nerve cells, which probably receives the impression, and it is quite likely that the adaption to distance depends upon the portion of this layer upon which the picture falls. I see no reason why the deeper cells should not receive an impression as well as the more superficial, and the difference of the focus cannot be very great. The whole internal surface of the ocellus is covered with pigment of a bright orange red color, and the three ocelli are connected with the cephalic nerve-centre by a single nerve.

The antennæ have the third joint remarkably dilated, but the others are comparatively little developed, except the last, which is very slender and covered with hairs. The third joint is covered all over with minute openings, which communicate with little transparent sacs or groups of sacs in the interior. The whole joint is lined with orange red pigment cells, and filled with a pulpy mass, which consists of the antennal nerve, minutely divided, and bearing multitudes of very small nerve cells, arranged like bunches of grapes at the extremity of its divisions. I believe myself that this is the organ of smell, although I by no means consider the antennæ of all insects are necessarily olfactory organs. I think in many instances they are merely feelers. Perhaps the beautiful feather-like antennæ of male moths are sexual ornaments, although they may have special olfactory organs connected with them ; and possibly the laminated antennæ of many beetles, which consist of thin chitinous lamellæ, may be hygrometric, indicating the state of the atmosphere to the insect. I have little doubt, however, in other insects, as in the fly, especially when they are thick and club-shaped, that they are olfactory, or rather partly olfactory organs.

The halteres are most evidently modifications of the posterior

## THE ORGANS OF SPECIAL SENSE.

wings, they are also called balancers, from an idea that they are connected with flight. A very large nerve, terminating in nerve cells fills their cavity, and is connected with a number of small, highly refracting bodies, regularly arranged around the base of the organ, which I am inclined to regard as otoconia, and if such is the case, the halteres are manifesty organs of hearing. That flies do hear, may be inferred from their possessing the power of emitting special sounds, and also by the manner in which they disappear when one is captured and allowed to make the peculiar plaintive note, which they invariably emit when distressed. In grasshoppers and other orthoptera, the organs of hearing are situated on the anterior tibiæ, so that the position of the halteres cannot be urged as an argument against such a function. A number of minute organs\* similar to those, which I believe to be otoconia in the halteres. are disposed in regular groups in the sub-costal nervure of the These are remarkably constant in insects, and are wing. especially interesting in relation to the halteres of flies, leading us, as it were, gradually up to the complete modification of the second pair of wings into organs of special sense.

The frontal sac may be connected with the sense of smell. The cephalo-sternum is a most remarkable organ, hitherto undescribed : and the lobes of the proboscis are probably the seat of taste, as they are largely supplied with nerves and have peculiar nippleshaped organs on their surface. The palpi are probably also concerned in taste when the food is regurgitated; and perhaps they assist the insect in its search for food as they are covered with minute openings with transparent sacs beneath, like those of the antennæ. Many of the hairs which clothe the various parts of the insect may also be endowed with special sense, as their bulbs are supplied largely with nerve filaments. I think it extremely pro-

\* These organs were first pointed out by Dr. Braxton Hicks, but their internal structure has not hitherto been described.

bable that their function is analogous that of the vibrissæ, or feelers of carnivorous animals.

## Section XI.—The Generative Organs.

The sexes are quite distinct in insects. The female fly is distinguished from the male by the great eyes being more nearly approximated and larger in the latter, as well as by the sexual organs. These consist in the male of a pair of testes, a pair of tubular glands, probably secreting an albuminous fluid, with their ducts; and of extremely complicated external organs, consisting of the four last abdominal segments.

The generative organs in the female consist of a pair of ovaries with their ducts. Three curious chitinous sacs which receive the male fluid, a remarkable receptacle containing two peculiar gelatinous masses after impregnation, beside a pair of tubular glands, which probably secrete the glutinous fluid with which the ovum is surrounded when it is deposited. The ova are fecundated at the time of deposition, and the larva is hatched twenty four hours after fecundation; but sometimes a single ovum is fecundated and retained within the ovipositor until the larva is perfected, and the insect is thus occasionally viviparous, or the egg is laid only a few seconds before hatching. There are three or four sets of ova contained in the ovaries, which are matured in succession.

The ovipositor consists of four joints, and is very long; it is introduced within the genital fissure of the male, during copulation, and it enables the insect to deposit its eggs in deep fissures, or beneath decaying matter. It is furnished with a pair of leaf-like appendages at its extremity, but has no hooks in the blow-fly, although that of the house-fly is furnished with a set of spines, pointed backwards around every ring.

## CONCLUDING REMARKS.

The ova undergo yolk segmentation, and just before impregnation, possess a micropyle, germinal disc, and yolk canal, just like the ova of the highest vertebrates. The skin of the larva is formed from delicate cells, and is complete eight hours after impregnation, but neither tracheæ nor viscera can be discerned so early; these are afterwards rapidly developed, and four and twenty hours after impregnation the larva escapes, its alimentary canal is filled with oil globules and molecular matter, and the tracheæ with air, at the time. The fat bodies are at this period scarcely perceptible, a number of delicate cells only being attached to the tracheæ. The larva commences immediately to feed, and increases rapidly in size, the fat bodies become largely developed, and at the end of three or four weeks it assumes the pupa state. Its further changes have been already described.

## Section XII.—Concluding Remarks.

The nervous system indicates that the Diptera, Hymenoptera Neuroptera and Orthoptera, are the most highly organized of all insects ; the presence of convoluted nerve centres supported by peduncles, and united by a commisure, which do not give off nerves, is an approach to the nervous system of the Vertebrata, and such nerve centres are perhaps the most important characters of the above mentioned orders. The elaborate modifications of the mouth in these orders for special purposes, the high development of the sense organs, and in the Diptera the remarkable modification of the posterior wings, and the articulation of the head with the thorax by a pair of condyles in some, point to a high type of organization. But at present it is extremely difficult to decide which of these orders is most highly organized ; they will probably eventually form a distinct sub-class of the insecta, characterized by its highly organized nervous system; and its divisions may perhaps be founded upon the various

degrees of metamorphosis, especially the presence or absence of imaginal discs in the larva, as suggested by Dr. Weismann; or upon the manner in which the head is articulated with the thorax, But until the types of other families have received the same attention as the fly, nothing certain can be said upon the subject.

In conclusion, it may not be out of place here to make a few observations on the position of the insecta in the animal kingdom. The highest insects should probably be regarded as the highest members of the annulose type; which is apparently so distinct from the vertebrate type that they cannot be compared with each other; for my own part I confess that I see no evidence of inferiority of type in either case, the structure of insects is as complex and their organs are as perfectly differentiated as those of the vertebrata. Professor Huxley has very ingeniously compaired the embryonic forms of the vertebrate and invertebrate types\* and supposes the nervous system of the insecta to be homologous with the sympathetic system of vertebrates, and that the cerebro-spinal nervous system and neural canal are added in the latter; such can hardly be the case if my observations on the nervous system of insects are correct, as they have also two distinct nervous systems. Even if such an homology should be substantiated, which appears unlikely, the supposition that the alimentary canal terminates anteriorly by a neural instead of a hæmal flexure would not explain the different development of the embryo from the entire surface of the yolk, and the fact that all the organs of manducation, prehension, locomotion, and the external organs of generation, originate from the lateral appendages of the various segments. No homologies can be traced for any of these organs between the insecta and vertebrata.

\* Introduction to the classification of animals,

# PART. II.

## DETAILS OF THE ANATOMY OF THE FLY

## Section I.— The Integument of the Head. PLATE II. FIGS. 1 and 2.

The head presents several regions which have been variously named by entomologists; the most important are the occipital or posterior, the frontal or forehead, the cheeks, and the facial, or that between the antennæ and the mouth. A correct appreciation of these will materially facilitate the description of the head. which, with its appendages, consists, as has already been stated, of five segments: of these however three belong to the proboseis, and three-fourths, that is the ventral and lateral plates of the fifth segment, are incorporated with the thorax ; so that the integument or external skeleton of the head itself consists entirely of the fourth, united with the dorsal plate of the fifth segment. The hard parts of the head are best examined by soaking or boiling it in liquor potassæ, drying it in hot turpentine and mounting it whole in a deep cell in canada balsam, without pressure: this will also be found the best method of examining most of the integumentary organs of insects with low powers ; it is troublesome at first, but becomes easy by practice

Some little difficulty may be experienced in realising the relations of the segments of the head, but by considering the

#### DESCRIPTION OF PLATE II.

This plate represents the hard parts of the head and proboscis, with the three anterior larval segments for comparison with those of the proboscis

Fig. 1. An anterior view of the head of the male, with the part belonging to the fifth segment colored; the hairs are removed and are represented only by their scars.  $\times$  10 diam

Fig. 2. Posterior view of the head of the female showing the greater width of the frontal plate; colored like the last.  $\times$  10 diam.

Fig. 3 and 3a. Ventral and side views of the hard parts of the mouth of the adult larva, consisting of a, the pharynx to which the appendages bb are attached; it is probably composed of the third segment united to the true pharynx, as in the perfect insect. The other parts are represented on a larger scale in figs. 4 and 4a,  $\times 25$  diam.

Figs. 4 and 4a. Ventral and side view of the first and second segment of the same. c, second segment. d, larval hooks or mandibles. e, labrum? f g, parts of the first segment, constituting the margin of the mouth.  $\times 7^5$ diam.

Figs. 5 and 5a. The triangular opening of the mouth of the perfect fly, seen from the front and side; a a, rudimentary mandibles; b, apodemes of the same; c, labium; d, labial appendages.  $\times$  75 diam.

Fig. 6. The labium and tongue.  $\times$  25 diam.

Fig. 6a. The apex of the tongue  $\times$  75 diam.

Fig. 6b. Section of the mouth, through the lower part of the operculum.

Fig. 6c. Section of the second joint, through the upper part of the operculum.

Fig. 7. The operculum composed of the labium and terminal lobes of the maxillæ, with their apodemes.  $\times$  25 diam.

Figs. 8 and 9. The mentum.  $\times$  25 diam.

Fig. 10. Scale-like basal lobes of maxillæ, with the basal bands bearing the maxillary palpi.  $\times$  12 diam.

Fig. 11. The fulcrum, consisting of the dorsal plate of the third segment the epistoma and the chitinious pharynx united, dorsal view.  $\times$  25 diam.

Fig. 12. The same with its muscles attached.

Fig. 13. Side view of the same, to show the attachment of the muscles; a, exsertor muscles; b, pharyngeal muscles; c, d, muscles to apodémes of the operculum ; e, muscles of salivary valve.

Fig 14. Section through the lower part of the pharynx, showing the central cavity and the disposition of the muscles by which it is opened.

. Figs. 15 and 15a. Small scale for protecting the bend of the pharyngeal tube, developed in the wall of the same.

Plate II





#### THE INTEGUMENT OF THE HEAD.

œsophagus as the axis around which they are arranged, it will be readily seen that the more anterior is horizontal and surrounds the base of the proboscis; its anterior extremity forming the boundary of the oral cleft, whilst the posterior is vertical, and is arranged around the cephalo-thoracic opening. The fourth segment bears the antennæ, and the fifth the ocelli; the great eyes also seem to 'elong to this segment, although externally they appear between the two; hence I shall call the fourth the antennal, and the fifth the optic segment, naming their dorsal plates respectively, from the positions they occupy, the facial and occipito-frontal plates.

Each of the plates which form the head will need a separate description. and as the dorsal plate of the fifth segment, the occipito frontal, is the centre around which the others are all arranged, it presents the fittest starting point : it is colored in figs. 1 and 2, Plate II. It commences at the superior and lateral margins of the occipital foramen, forms the central portion of the occipital region, and then bends forwards and downwards, forming the forehead, and divides into two lateral processes, which bound the lower margins of the great eyes and terminate by becoming intimately blended with the cheeks. The line of division is indicated only by a more or less perceptible ridge, but it is well marked in several of the Syrphidæ. I do not think, however, that the blending of the two segments in this region would afford the slightest argument against their distinctness, as it is in the dorsal region that we first find the segments become blended with each other, and as already stated, the two correspond ing segments in the larva are united into one above. It is true that the anterior edge of this plate is only loosely attached to the dorsal plate of the fourth segment (the facial plate) by a membrane, but then this membrane, as will hereafter appear, serves a special purpose, and the union of the dorsal plate of the fifth with the lateral plates of the fourth segment, gives the chief strength to the anterior portion of the head. On each side of the occipital foramen the occipito-frontal plate is hollowed out into a cup-shaped depression to receive the apex of the conical condyle, which steadies the head, and which consists of the lateral plate of this segment.

Below the occipital foramen is the basilar plate, the ventral or inferior portion of the fourth segment; it bears a pair of internal processes, which support the cephalic nerve-centre and the main tracheæ of the head.

The lateral plates of the fourth segment are very large, as they compose the greater part of the occipital region, and bend forwards to form the cheeks, where they bear a number of strong hairs.

The dorsal plate of the fourth segment, the facial plate, bears the antennæ at its superior or curved margin, which corresponds with a concavity in the anterior margin of the occipito-frontal plate; inferiorly it is continuous with the proboscis; its inferior angles are united to the checks, and the remainder of its margin is continuous with the membrane already referred to, which attaches it loosely to the occipito-frontal plate.

When the perfect fly emerges from the pupa, a large protuberance occupies the front of the head immediately above the antennæ. It consists of a membrane, by the dilatation of which the insect bursts off the anterior extremity of the pupa case; when fully dilated it is larger than the head, which is as yet retained within the pupa; but as soon as the latter escapes, this protuberance rapidly collapses and is withdrawn into it. Until the integuments are thoroughly hardened it may be made to protrude from the head by gentle pressure, but is not afterwards visible externally; by pressing back the facial plate, however, a fissure is opened between it and the occipito-frontal plate and cheeks, by which the cavity formed by the retraction of the membrane communicates freely with the external air. The membrane is continuous with the integument at the margins of the fissure ; it assumes a bright yellow color in the mature insect, and is thrown into numerous plications ; its connections are best seen from the interior of the head. The extent of its surface is very great, and is much increased by being closely covered with papillæ. It has probably three distinct functions : first, it serves to break off the anterior extremity of the pupa case; secondly, it is undoubtedly connected with the humming of the insect, the facial plate being thrown into rapid vibrations during the emission of sound; and lastly, it seems to receive numerous nerve filaments from the antennal nerves, and is probably an accessory organ of smell. From its position I propose the term frontal sac to designate it.

#### THE PROBOSCIS.

# Section II.—The Proboscis. PLATE II. Figs. 3—15. PLATE III.

The probose is is one of the most remarkable and complex structures found in the insect world; it consists of three joints, each of which represents a distinct segment. Its hard parts are the homologues of those usually found in the mouths of insects, and although they are greatly modified to serve special purposes, yet, owing to the elongated nature of the organ, the several segments are perhaps more decidedly distinct in the fly than in any other insect.

The integument of the basal joint consists chiefly of a funnelshaped membrane continuous with the antennal segment around the oral cleft; a semi-transparent trapezoidal plate of chitine, the epistoma, which forms a hinge with the facial plate, is developed upon its dorsal surface, \* (it is represented in outline in Plate II. Figs. 11 and 12). Connected with the inferior edge of this and almost entirely enclosed within the funnel-shaped integument, a very complicated organ is found; it is the largest piece in the proboscis, and forms a fulcrum upon which all the other parts move. It gives attachment to five pairs of muscles and guides all the movements of the basal joint, which is otherwise membranous. The walls of this organ are double, and the two plates are kept in apposition by their elasticity, but are capable of being separated and of forming a cavity by the action of a pair of large muscles, the cavity so produced being continuous

\* In order to avoid repetitions, it is to be understood that the words dorral and ventral, as applied to the proboscis, relate to the surfaces which assume those positions when the organ is extended and drawn forward; anterior and posterior likewise refer to the same position of the organ, that which it would assume if the cosophagus were straight instead of curved in the head.

anteriorly with the mouth, and posteriorly with the œsophagus. The dilatation of this cavity draws fluid from the mouth, and its obliteration which is entirely effected by the elasticity of its walls, injects it into the œsophagus and sucking stomach or crop, the absence of valves being made up for by the peculiar rythmic action of its muscles, the anterior fibres contracting and again relaxing before the posterior, so that an undulating motion is given to the superior wall of the cavity. Although I believe this organ is homologous to the fulcrum in bees, I prefer the term pharynx, from its double connection with the mouth and œsophagus, as well as its peculiar function. (It is represented in Plate II, Figs. 11, 12, 13, 14 and Plate III. a.)

The pharynx or fulcrum consists of a body and four processes, and the body of a dorsal and ventral arch; the dorsal arch is continuous with the integument, and is united above with the trapezoidal plate, which I have called the epistoma, of which it probably forms a part; the ventral arch is more properly pharyngeal, being probably developed in the walls of the alimentary canal and not belonging to the integument; it consists of two layers, between which the cavity connecting the mouth and the œsophagus is situated. The superior, or dorsal layer, is thickened in the mesial line, forming a rod of chitine, which extends beyond the inferior plate at its anterior extremity. On either side of this a row of fine setæ project into the interior of the cavity, their points being turned towards the cesophagus; these are probably sensory organs by which the act of swallowing is controlled. The inferior layer is thicker and stronger than the superior, and gives strength to the whole organ. The hollow between the ventral and dorsal arches is occupied by a pair of sets of muscles, which arise from the inferior part of the dorsal arch, and from the dorsal edges of the ventral arch, and are inserted into the mesial line of the superior layer of the pharyngeal tube, which they separate from the inferior by their contraction. They are remarkable in containing a large number of branched muscular fibres.

The posterior processes give insertion to the exsertor muscles of the probose, (Plate II, Fig. 13 a) which arise from the interior of the cheeks. In order to understand their action, we must consider the position of the pharynx when the probose is retracted. It is then withdrawn into the cavity of the head and lies with its posterior processes against the upper part of the facial plate, and its anterior or distal end against the inferior (posterior) margin of the oral cleft, so that its direction is almost horizontal, the epistoma being folded back on the facial plate. The contraction of the exsertor muscles draws down the pharynx and causes it to revolve upon the junction of the epistoma and facial plate.

#### THE PROBOSCIS.

At the anterior part of the basal joint a pair of bands partially surround the proboscis (Plate II. Fig. 10, and Plate III. e.) These bear six or eight stiff setæ, which act as vibrissæ or feelers. The great maxillary palpi are attached to the upper part of the posterior edge of the bands, the anterior edge of which is continuous with a thin scale, covered with curved hairs. The scales and bands are undoubtedly homologous to a part of the maxillæ of other insects. The remainder of the maxillæ seems to be united with the labrum and to be supported by a pair of lever-like apodémes or internal processes, which lie one on either side of the pharynx, between it and the bands in question. (Plate II. Fig. 7.)

I believe the basal joint of the proboses, with the epistoma and maxillæ, form the third segment in both the larval and perfect forms of the fly. In grasshoppers, the three segments, formed by the facial plate, the epistoma and the labrum, are quite distinct in front and correspond exactly to the parts I have so named. Moreover, the maxillæ clearly belong to a segment posterior to that which bears the mandibles, not only in the fly but in other insects. This is quite plain in the cockroach. The position of the labium, which consists most undoubtedly in great part of a pair of modified limbs, indicates that it forms the most anterior segment of all.

The homology of the maxillæ needs careful study and comparison with other insects. In bees, especially Xylophaga, these organs consist of a basal sheath, which partially surrounds the pharynx and bears a comb of stiff teeth, as well as the palpi. Two lobes arise from this sheath, a small superior one covered with hairs, and a large sharp-pointed spathulate lobe with a straight superior edge, fitting against that of the opposite side, and forming the upper lip. The band in the fly represents the basal sheath, and the comb of bees is replaced by the setæ. The thin membranous scales are homologous to the small superior lobes, and the long pointed scales united in the fly to the labrum are clearly the homologues of the terminal lobes in bees, although they have usually been described as the mandibles. My friend Mr. C. Stewart pointed out to me that the thin scales homologous to the superior lobes are united with these organs in Rhingia, an arrangement which seems common in the Syrphidæ, and which puts the matter, I think, beyond a doubt.

The pharynx and maxillæ are both represented by corresponding organs in the larva, (Plate II. Figs. 3 and 3a, a and b.) The sucking organ a, both in function and form, is too like the same

part in the perfect insect to doubt its homology. The small straight appendages bb, appear to belong to this organ, which supports them, and to represent the maxillæ. I am even inclined to believe the superior ventral processes of the sucking organ are the homologues of their apodémes, No connection can, however, be absolutely traced between these parts in the larva and perfect insect, as all parts of the mouth of the former remain attached to the pupa case, but I am inclined to believe this is a mere shedding of integument, and that the new organs of the mouth are directly dependent for their formation upon the old, like the abdominal segments and the whole digestive system.\*

The second segment of the proboscis (Plate III) folds upon the basal one with an elbow-like joint, so that their dorsal surfaces are in contact when the organ is at rest. The maxillary palpi then lie against the edges of the oral cleft, and are directed

#### DESCRIPTION OF PLATE III.

This plate represents the right half of a vertical section of the proboscis a little to the left of the mesial line. a, The pharynx, cut through above but not divided vertically. b, The operculum, with one of its apodémes, which may be traced behind the pharynx. c, The labium, which forms the floor of the mouth and is continuous above with the salivary tube. d, Half the mentum. e, Band supporting the scale-like lobe of the maxilla, several setæ, and the maxillary palpus. f, Valve in the salivary duct. g, Great tracheal sac giving off the main tracheal vessel, which supplies the muscles of the canula and lobes. h, The lobes, with some of the hexagonal pigment cells shown as well as the spherical cells, to which the greater portion of the main nerve-which accompanies the principal tracheal vessel-is distributed. i, Chitinous band surrounding the triangular opening of the mouth, which supports the false tracheæ and the tecth; its anterior extremities bear a pair of curved hooks, probably the homologues of the mandibles. A group of spherical cells, immediately connected with a set of recurved hairs, is seen above this piece, with a branch of the main nerve distributed to them.

\* Weismann asserts (Koll. Zeitschrift, Band. XIV.) that the salivary glands of the perfect fly are new formations, and that he once found the salivary gland of the larva by the side of that of the perfect insect, in the same imago; I think, however, the malformation must be otherwise accounted for. See Section III. page 51.





#### THE PROBOSCIS.

forwards, occupying exactly the same position as in the Lepdoptera. Whatever their function may be, it is probably called into activity when the proboscis is retracted, for they are turned back when it is exserted; they are probably connected with the sense of taste or smell.\*

The second joint consists of two portions, one dorsal and the other ventral, the former being the roof, and the latter the floor of the cavity of the month; so that they might well be named lips, if the term had not been unfortunately applied to the terminal lobes of the proboscis; especially as the upper consists of the labrum and terminal lobes of the maxillæ, and the inferior of he united labium and mentum. I shall call them respectively the operculum, and the canula.

The canula is thick and fleshy, being filled with muscles; it is terminated by the lobes of the probose is, and is deeply grooved on its dorsal surface, the groove forming the mouth, and concealing the tongue. The edges of this groove overlap the operculum, and completely cover its anterior extremity, meeting in front of it, so that it is held firmly in its place, but by a little violence it can be made to start upwards and assume a position at an angle with the canula, without any rupture of membrane. It never leaves the groove, however, during life, although in those diptera in which the maxillæ, mandibles, and tongue form lancets, the canula is capable of being folded back, to bring the lancet into play.

The operculum, Plate II, Fig. 7, consists of a central and two lateral portions.

The labrum or central part is tubular behind, and is united by a membranous tube to the anterior extremity of the cavity of the pharynx, a small semicircular piece of chitine protecting its bend; the food passes from the mouth by this means into the pharynx. The anterior two-thirds of the labrum is open below and forms the roof of the mouth.

The homologies of the lateral portions of the operculum have already been discussed.<sup>+</sup> They are firmly attached to the back of the labrum and form,

\* See Section IV. page 55, and XV. page 93. + Page 43.

joints with their apodémes, which give insertion to two pairs of muscles both arising from the pharynx. Plate II, Fig. 13, shows the points of origin at c and d; both are inserted into the free extremity of the apodème; they are probably flexors of the second upon the first joint of the proboses. They act by drawing the head of the apodéme towards the dorsum and pressing it forward; as the apodémes act upon the operculum slightly behind the line of flexion, they press its superior extremity downwards and forwards, causing its anterior extremity to revolve in the opposite direction. The whole of the interior of the operculum is lined with epithelial cells containing bright red pigment.

The canula consists below of the mentum, a shield-like plate bearing a pair of processes at its anterior extremity, which keep the lobes of the proboscis closed by their elasticity; a small triangular plate unites them inferiorly. The whole superior surface of the mentum gives origin to muscles. The largest pair being inserted into the terminal processes serve to open the lips. A pair of thin muscular slips arising from the margin of the occipital foramen is inserted into the posterior margin of the mentum. The latter are retractors of the whole proboscis as well as extensors of the second joint. The edges of the mentum are everywhere united to the membranous sheath of the proboscis.

Tracing the membranous covering of the canula from the edges of the mentum, it is found to become chitinous in the groove on its upper surface and round the anterior extremity of the mouth, forming the base of the great lobes; these parts represent the labium or lower lip of which the last named are lateral appendages. Perhaps the labium is the most difficult organ to understand in the mouth of insects. It consists of five distinct parts, if the tongue be considered as a portion of it, and these seem to be very constant. They are 1, the floor of the mouth united to the upper side of the mentum; 2, the tongue united to the posterior extremity of the floor of the mouth, but more or less free in front ; 3, a plate attached to the anterior border of the floor of the mouth in front of the mentum; 4, a pair of palpiborne by the base of the last part on its inferior surface which are turned downwards; 5, a pair of lobes turned upwards and borne by the extremity of the same plate : these are the modified limbs which belong to the most anterior segment. All these parts may be distinguished in the labium of the fly, except the palpi. Much confusion exists as to their nomenclature especially between the last-named and the tongue, both having been called the ligula. I shall call them respectively

the posterior labial plate, the tongue, the anterior labial plate, and the labial appendages or lobes.

The posterior plate of the labium, (Plate II, Fig. 6, c, and Plate III, c,) replaces the membrane at the bottom of the groove in the canula. It forms the sides and floor of the mouth. Two lateral rods are interposed between it and the operculum anteriorly; but behind, it fits against the operculum, as far back as that part is incomplete. Where the operculum becomes tubular the labium also becomes closed above, and is continued backward united with the tongue, as a tube which joins the salivary duct. The tongue, (Plate II, Figs. 6 and 6a,) is tubular behind and united to the labium, but becomes thin and lancet-shaped in its anterior third, before the opening of the salivary tube. Its free extremity is covered with fine setæ.

The posterior plate of the labium is probably part of the mental or second segment. Its inferior surface has a number of muscular fibres inserted into it, which arise from the mesial line of the mentum. On either side of the posterior plate of the labium is a rod, (Plate II, Fig. 6 b,) united to it in the mature fly, but quite distinct when the insect first emerges from the pupa. These rods support a pair of hooks, (Plate II, Figs. 5 and 5a,) which, on comparison with the larval hooks (shown in Figs. 4 and 4a in the same plate,) will be found to correspond very nearly to those organs. I am inclined to believe they are the homologues of the mandibles, and therefore the lateral appendages of this segment. The larval hooks are supported by an H-shaped organ, (Fig. 4 c.) which seem to represent the second segment, and I have found the same rods and hooks in all the Diptera which I have examined, in which the larva are furnished with hooks. Like the maxillæ and labial lobes they are placed on the dorsal aspect, and in front of the segment to which they belong. There is no other representative of the mandibles.

The third segment of the proboscis (Plate III, h. i.) consists of the margin of the anterior opening of the mouth, which is triangular, and of the large fleshy lobes at its extremity. These when at rest are folded against each other, but when they are opened, about two-thirds of their anterior surface forms an oval sucker divided into two parts by the fissure between them. Behind this fissure the remainder of the lobes forms a cavity bounded posteriorly by the triangular opening of the mouth.

The anterior surface of the lobes is channelled by a series of canals,—kept open by incomplete rings,—called false tracheæ, which open internally into the cavity between the lobes and so into the mouth; these form a fine strainer through which the in-

sect is enabled to filter the fluid from the solid portion of the substances on which it feeds. The lobes are, however, capable of further separation, exposing the triangular opening which is surrounded by from fifty to sixty bidentate rods or teeth, which are usually concealed between the posterior portions of the lobes but are used, when exposed, for grinding hard substances, such as sugar, so assisting the salivary secretion to dissolve them<sup>\*</sup>. Fluids are often drawn directly into the mouth, either by the fissure between the lobes when it is partially closed, or even when it is fully opened to expose the teeth, but they more usually pass through the false tracheæ. This is best demonstrated by giving the fly a little blood and afterwards examining the proboscis, when all these channels will be found filled with it.

The parts forming the anterior triangular opening of the mouth are represented in Plate II, Figs. 5 and 5a; they are a dark solid mass of chitine and two lateral plates, which probably represent the anterior labial plate and the basal portion of its lateral appendages; they bear the lobes and bidentate rods or teeth, already mentioned,

The false tracheæ, (Plate IV, Figs. 2 and 3,) are channels on the anterior surface of the lobes, kept open by semi-rings, which are developed from cells of the protoderm. These rings are bifurcated at one extremity, and the bifurcated extremity is alternate in the several rings<sup>†</sup>. The channels become gradually smaller towards the edge of the disc and terminate in closed extremities. Their number is variable and not always the same of the two sides of the proboscis; there are generally twenty-nine or thirty on each side. They usually open on the inner edge of the lobes in the following order. The five anterior channels unite and form a large trunk, which runs along the upper border of each lobe and opens close to the upper margin of the triangular opening ; the next seven or eight open separately, each externally to a set of teeth, and the remainder run into a pair of parallel channels in the middle of the disc below the opening of the mouth, which open at the lower part of the triangular opening. Between the margin of the triangular opening and the orifices of the false trachcal channels, a number of curved chitinous pillars are found radiating from the sides of the triangular opening to these orifices ; they are distinctly seen to represent the semi-rings of the channels themselves flattened out.

\* Some very interesting information on this subject with good figures of the details of the false trachcæ, is given by Mr. W. T. Suffolk, in a paper read before the Royal Micros. Soc. Ap. 14. 1869.

\* Described by Mr. Hunt, Microscopical Quarterly Journal, 1856, p. 238.

#### THE PROBOSCIS.

Between each pair of false tracheæ the surface of the lobes is marked by a pair of wavy lines; these are folds of the integument, and disappear when the membrane between the false tracheal channels is stretched. Four or five nipple-shaped papillæ project from the surface, between each pair of wavy lines, and nerve filaments terminate in them; they are probably Organs of taste. The disposition of these parts is shown in section, in Plate IV, Fig. 3.

A row of cells around the margin of the lobes are hardened into little square plates; these are developed in the membranous protoderm; several other, but less developed, rows of a similar nature extend towards the back of the lobes.

The mesoderm consists of beautiful nucleated pigment cells, filled with a bright orange-colored pigment; in the mature insect these are united into a continuous membrane; their nuclei become apparent on the addition of a little acetic acid.

The back of the lobes is covered with hairs, which form a fringe around its disc. The endoderm consists of numerous spherical cells, containing granular nuclei, and the bulbs of these hairs, with a plexus of nerve  $loop_s$ distributed to them, from the terminal branches of the great nerve of the proboscis. A group of recurved hairs with a similar plexus of nerve loops is situated on each side of the second joint, near its anterior extremity.

The false tracheal channels are partially surrounded at their orifices by the curved extremities of the chitinous pillars which support them upon the anterior border of the mouth. Closely connected with the points of these, and immediately beneath the integument, is a tendinous looking band of dense tissue, which extends the whole length of the fissure between the lobes of the proboscis. A round cord of similar tissue arises partly from this band, and partly from the point of the chitinous pillar, on either side of each false tracheal channel. The pair which arise from each pair of points unite and form a thicker round cord, which runs outwards towards the margin of the lobe, near which it is inserted into a thickened ridge of chitine, connected with the anterior extremity of the anterior process of the mentum, at right angles to it. The purpose of these cords seems to be to connect the extremity of the anterior processes of the mentum with the margins of the fissure between the lobes, which is proably kept closed by the elasticity of the pillars which support the orifices of the false tracheæ, and which is opened by the muscles attached to the anterior processes of the mentum, through the agency of these tendinous bands. If these processes of the mentum acted upon the margin of the fissure by drawing upon the integument of the lobe, the margin of the sucker, formed by the union of the lobes, would have been disturbed in order to open the fissure; whilst, by means of these bands, the anterior process of the mentum not reaching the margin of the lobe, acts directly

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upon the fissure, without impairing the action of the sucker or altering the position of its edge. These bands are dissolved by liquor potasse, they exhibit a dark outline; do not swell up when treated with acetic acid and are elastic. They are developed from spindle-shaped nucleated cells, which may be found in great numbers in the lobes of the proboscis of the immature fly.

There is no better method of examining the proboscis, in order to obtain a general idea of its structure and functions, than by observing that of a living fly whilst in action. This may be conveniently done by enclosing the insect in a live-box, with a few spots of syrup on the thin glass cover, and illuminating it from above. This method was first suggested by the late Richard Beck. Another very good way of examining the entire organ, is to take a recently killed fly; exsert the proboscis by pressing on the thorax, and tie its base to keep it distended. It may then be examined dry, or mounted in glycerine, in which it becomes a very beautiful object, when it has soaked in that medium a sufficient time to become transparent, especially if illuminated by a black spot lens, as recommended by Mr. Suffolk. This method is subject to the grave objection that specimens so obtained are unnaturally tumid, and assume an appearance quite unlike that natural to the organ. Sections of the proboscis made with a lancet, or the entire organ cut off and mounted in glycerine, are the most instructive specimens, and are the only means of making out the minute anatomy of the part. Those required to show the distribution of nerves should first be hardened in spirit, or chromic acid. Numerous recent sections should be examined as well as mounted specimens. Mr. Topping's well-known and beautiful preparation only exhibits the chitinous parts, and the mentum is cut away in order that the lobes may lie flat : although most useful as a means of examining the structure of the false tracheal channels and the teeth, the relations of the parts are so altered by pressure, that some cannot be made out at all. All the hard parts may be seen in situ by treating the whole head, with the extended proboscis, in the manner already recommended for examining the integument of the head; but it is very difficult

to mount a perfect specimen, as the lobes of the proboscis usually collapse.

## Section III.,—The Salivary Glands and Ducts. PLATE III. f. PLATE IV. Figs. 1 and 6.

The salivary glands consist of a pair of long convoluted tubes which lie one on either side of the chyle stomach in the thorax and extend into the abdomen, terminating near its apex in blind extremities. (They are shown in situ in Plate I, and in their relation to the alimentary canal in Plate IV, Fig. 1.) Each gland tube opens near the posterior portion of the thorax into an elongated sac, which its convolutions closely surround. This sac is lined with delicate pavement epithelium, and terminates anteriorly in the duct. The salivary ducts converge and unite in the thorax just behind the cephalo-thoracic opening, forming the common salivary duct. This enters the head beneath the œsophagus, which it immediately leaves, and passes between the pharynx and membranous integument of the basal joint of the proboscis, finally opening on the upper surface of the tongue.

The salivary glands of the larva consist of elongated sacs, lined with coarse pavement epithelium. I think there can be little doubt but that the sacs of the glands in the perfect insect are dependent for their formation on the salivary glands of the larva, the epithelial coat having alone under-gone change. Dr. Weismann asserts that he once found a fly in which he detected the larval salivary gland by the side of that of the imago. I can only understand his assertion by supposing the malformation in question was due to the salivary apparatus of the larva having been double in that specimen, only one of the glands having undergone the usual changes. I once found the sacs of the salivary glands of the adult fly lined with the same epithelium as the larval salivary gland, but only once.

The tubular portion of the gland in the fly is filled with gland cells; and its external coat is covered with a plexus of tracheal vessels, (a portion is represented in Plate IV Fig. 6). The whole length of each tube if unwound would exceed two inches, or nearly four times the length

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of the entire insect. The gland cells are 1-1000th of an inch in diameter.

The salivary ducts and common salivary duct are kept open by a spiral fibre, developed in their internal coat. The external coat is yellowish, thick, and thrown into rugæ, except when the ducts are stretched. The ducts are exceedingly elastic and extensile. Just above the labium the common duct changes its character, losing its spiral fibre and extensibility. It becomes perfectly transparent and dilates into a cavity somewhat resembling the human glottis. This is a most perfect valve; for its superior\* wall is elastic and pressed down at its anterior portion against the inferior wall, so entirely closing the duct at this point. A pair of long slender muscles, arising at the posterior extremity of the pharynx, run beneath that organ, and are inserted into the anterior part of this valve, opening it by their contraction.

It will be easily understood that the sucker-like action of the lobes as well as the opening of the pharyngeal cavity, would tend to exhaust the mouth of air, and so to cause a flow of salivary fluid into its cavity, which would continue as long as the proboscis remained in action, were it not for this valvular arrangement in the salivary duct. The opening and shutting of the valve is controlled by a ganglion placed in front of and beneath it. Nerves from this ganglion are distributed to the mouth, as well as to the long muscles which act upon the valve. Any dryness of the epithelial lining of the mouth, in which these nerves ramify, would undoubtedly communicate an impression, and cause a reflex act by which the valve muscles would contract, and so cause a flow of saliva by opening the valve.

<sup>\*</sup> See note to page 41. These relations may be observed in Plate III but the lower portion of the plate, it must be remembered, represents the anterior extremity of the proboscis, and the left side its dorsal or upper surface.

## THE ALIMENTARY CANAL AND ITS APPENDAGES.

## Section IV.—The Alimentary Canal and its Appendages. PLATE IV. Figs 1 – 8.

The œsophagus commences at the posterior extremity of the pharynx, and curving sharply backwards, pierces the cephalic ganglion and passes through the cephalo-thoracic opening, above the great nerve trunk, and beneath the dorsal vessel. As soon as it enters the thorax it divides into two branches of equal diameter. One passes upwards and immediately opens into the proventriculus; the other runs the whole length of the thorax, beneath the chyle stomach, and passes into the abdomen under the intestine, above the great nerve, and between the salivary glands, to all of which it is closely bound by a plexus of tracheal vessels, in the meshes of which the nerve cells of the great sympathetic ganglion lie. As soon as it enters the abdomen it opens into the sucking stomach or crop.

The œsophagus may be said to have four coats; the most external of circular and the second of longitudinal muscular fibres; the third consists of membrane insoluble in liquor potassæ; and the fourth of pavement epithelium. The membranous coat exists throughout the whole alimentary canal, and bears the epithelial lining; like the protoderm it is continuous, and insoluble in hot solutions of caustic potash. I have no doubt that a new layer is formed in the pupa on the exterior of the old, which is shed like the integument of the larva, but this has not been demonstrated; it differs from the protoderm in developing epithelial cells upon its free surface, but I believe it is continuous with it.

The sucking stomach consists of a pair of almost hemispherical sacs, united anteriorly in the mesial line; it serves as a reservoir for the food when first taken. There is no organ homologous to this stomach in the larva, but it is developed from a bud which appears in the pupa on the under side of the œsophagus. The organ in the maggot which performs the same function is a large flask-shaped sac, which opens directly into the pharynx, and the œsophagus commences from the under side of its neck. The neck of this sac is not surrounded by the great ganglia, but is anterior to them; and the sac is dorsal to all the other organs in the larva. When the maggot is feeding

it appears upon the back as a dark egg-shaped mass; it shrivels gradually after the larva ceases to feed, and disappears entirely before the third day of the pupa state; I shall call it the pharvngeal pouch.

In the sucking stomach the external or muscular coat consists of interlacing muscular bands, which terminate in pointed, and often in

#### DESCRIPTION OF PLATE IV.

Fig. 1. The alimentary canal, as it appear after the insect has been fed on food mixed with cochineal. The asophagus and crop are filled with fluid, coloured with the pigment. In the chyle stomach the food assumes a violet colour; the salivary glands remain uncoloured and present a transparent blueish tint. The bile tubes are only partly shown, with their ducts filled with yellow bile pigment, and the rectal papille are deeply stained with cochineal.  $\times$  12 diam.

Fig. 2. A portion of one of the false tracheal channels of the proboscis; the protoderm is torn away from the edge of the channel at its right extremity, to show the manner in which it is folded.  $\times$  500 diam.

Fig. 3. A section through a portion of the surface of one of the lobes of the proboscis; showing a false tracheal channel cut through transversely, and the folds of membrane between it and the next channel with one of the nipple-shaped papillæ between them.  $\times$  500 diam.

Fig. 4. Side view of the anterior extremity of the chyle stomach; showing the proventriculus and the sacculated walls of the chyle stomach.  $\times$  36 diam.

Fig. 5. Cylinder epithelium from the chyle stomach.  $\times$  250 diam.

Fig. 6. A portion of the salivary glands, to show the ramification of the tracheal vessels and the disposition of the gland cells.  $\times$  250 diam

Fig. 7. A portion of one of the Malphigian or liver tubes.  $\times$  250 diam.

Fig. 8. The valve between the large intestine and rectum.  $\times$  36 diam.

Fig. 9. A vertical section of one of the rectal papillæ or renal organs.  $\times$  60 diam.

Fig. 10. Gland cells from the same.  $\times$  250 diam.

Fig. 11. The apex of the same.  $\times$  250 diam.

Fig. 12. A transverse section of the same. x 60 diam.





#### THE ALIMENTARY CANAL AND ITS APPENDAGES.

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branched extremities. This coat is thickest near the opening of the œsophagus, and the fibres of that portion of the organ which lie in the mesial line are mostly circular. Numerous nerve cells belonging to the sympathetic system are scattered over the external coat, and form a pair of large patches, near the entrance of the œsophagus. The cavity of the sucking stomach is lined with pavement epithelium, and frequently contains a beautiful mould, allied to Botrytis, which often causes the death of the insect by its rapid development.

The proventriculus is a small globular cavity at the commencement of the chyle stomach (Plate IV, Fig. 4,); it has thick glandular walls, and secretes the gastric fluid; it opens directly into the chyle stomach, where absorption commences. The epithelium of the proventriculus consists of several layers of clear nucleated cells, those upon the surface being angular and closely adherent to each other; the deeper layers are oval, and the most external float freely in fluid. They differ remarkably from the epithelium of the chyle stomach, which consists of a single layer of conical cells. This is especially noticeable in the larva, where the epithelium of the chyle stomach is opaque with granular matter : whilst the gland structure of the proventriculus is perfectly transparent. The proventriculus of the larva is larger and more oval than that of the imago.

The proventriculus may be said to consist of an intussusception of the œsophagus, the muscular coat disappearing in the middle of the organ, and the membranous coat being reflected back upon it and swelling out to make room for the thick glandular lining. It is again constricted at the commencement of the chyle stomach by a muscular sphincter. The tracheal vessels, which ramify in a close net work over the membranous coat, dip down into the interior with the œsophagus ; and then take a radiating direction. It has a larger supply of tracheæ than any other part of the alimentary canal.

The analogy between the functions of the crop proventriculus and chyle stomach, and the crop rennet and paunch of Ruminants is too obvious to need enlarging upon. But the resemblance of the digestive act in the two cases is even closer, for the fly frequently brings its food back into the mouth, probably for the purpose of mingling it with the saliva. I have repeatedly observed flies exude a large drop of fluid from the oral cleft without exserting the proboscis, and gradually reimbibe it. As such a drop entirely surrounds the palpi, I think it not unlikely they are the organs of sensation concerned in this act, and perhaps the seat of the special sense of taste. In the larva the food passes directly from the pharyngeal pouch into the proventriculus.

The chyle stomach extends the whole length of the thorax ; it is divided by reticulations of circular and longitudinal bands of muscular fibres, between which the membranous coat bulges, so that its inner surface is covered with little square pits. It is lined with conical cylinder epithelium. It is much longer in the larva than in the perfect insect, and four exceal glands, about half its length, open into its anterior extremity. These disappear in the pupa, and are not redeveloped in the imago.

The small intestine extends from the stomach to the opening of the bile tubes, about three quarters of an inch; its upper end is like the chyle stomach, which passes insensibly into it, but it soon looses its reticulated structure, and its muscular coat becomes uniform and thin. Both circular and longitudinal muscular fibres may be traced in it.\* In the larva the bile tubes open at the posterior extremity of the stomach, and the small intestine first appears in the pupa.

The bile tubes (Plate IV, Figs. 1 and 7) commence in blind extremities, and unite in pairs, until they open into the intestine, by two large ducts. They are very numerous, and occupy the dorsal portion of the abdomen; they have a beaded outline and contain irregular nucleated cells, yellow pigment, and fat granules. I have found occasionaly dumb bell crystals in the bile tubes, but have failed to detect uric acid in them, either in the larva or imago.

<sup>\*</sup> Its peristaltic action is very vigorous and may be observed plainly in the smaller house fly, the sides of the abdomen of which are very transparent. It may be seen also in the immature Blow-fly.

## THE RECTAL PAPILLÆ.

The large intestine is about four lines in length in the perfect insect, but exceeds an inch in the larva; it extends from the openings of the bile tubes to a double muscular sphineter or valve, which separates it from the rectum. It differs considerably in structure from the small intestine. Its muscular coat, especially the longitudinal fibres, is much more largely developed and its middle or membranous coat is covered on its internal surface with a number of sharp spines, with broad bases, which project downwards, and somewhat resemble narrow shark's teeth. These processes become more blunt at the valve, between the large intestine and the rectum, and extend into the upper portion of that intestine; they afford an additional argument in favor of the membranous coat being continous with the protoderm. Both the large intestine and the rectum are lined with ordinary mucous tesselated epithelium.

The rectum dilates into a pyriform cavity, just below the recto-colic valve, which contains the rectal papillæ. Below this dilatation it becomes again constricted, and a well developed sphincter of circular fibres may be observed close to its outlet. It opens at the upper part of the last joint of the ovipositor of the female at its extremity, and in the male it terminates above and behind the penis.

The viscera may be carefully examined in situ, by partially imbedding the insect in wax, and removing those parts of the integument which are not imbedded, with a pair of fine scissors.

## Section V.—The Rectal Papillæ. PLATE IV. Figs 9 to 12.

The organs for which I have retained the name given to them by Weismann, are four in number, situated near the termination
of the alimentary canal. They are hollow, conical, glandular organs, about 1-30th of an inch in length, enclosed in the dilated portion of the rectum, and having their bases only external to its cavity. Their function is probably the excretion of a urinary fluid.

Each papilla consists of three parts (Plate 1V, Figs. 9 and 12): an internal central cavity, surrounded by a transparent structureless membrane; around this a hollow cone of gland cells, the secreting portion of the organ, is disposed; and external to this again, a tough transparent cone of membrane, which I shall call the calyx of the papilla. perforated by numerous minute pores, surrounds the whole of that portion of the organ which is internal to the rectum. By a little dexterous manipulation these parts may be separated completely from each other, or, by hardening the papillæ in chromic acid, sections may be made showing the relations of the parts in situ. Fig. 9 represents such a section.

The calyx is perforated by about 300 minute pores, each pore being surrounded by a nipple-like projection, which is surmounted by from three to eight minute setæ, (Plate IV, Fig. 11). The whole membrane of the calyx becomes thickened towards its apex, where it has a faint, yellow tint; it is near the apex that the nipple-like projections and their setæ are best seen. Indeed a casual observer might overlook their presence entirely at the upper portion of the calyx.

The calyx itself is marked by faint reticulations, and its margin is deeply crenated. These are the only indications of structure which it presents, and these seem to point to its being a fibrous membrane, especially as two sets of muscular fibres arise from the crenations of its margin.

These muscular fibres are, first, a set from the muscular coat of the rectum, and, secondly, a layer of converging fibres which cover the whole base of the papilla to within a very short distance of its centre, and which apparently end in the edge of the membrane forming the boundary of the central cavity, although from the extreme transparency of this membrane it is nearly impossible to be certain of their insertion.

Each papilla is supplied with air by a large tracheal vessel from the fifth abdominal spiracle, which divides into several—generally five or six large trunks before entering the papilla. The tracheæ of the papilla may be divided into two sets as soon as they enter the base of the organ. First, from twenty to thirty radiating lateral branches run to the edge of the base, and then pass over the outer surface of the glandular structure to the apex of the cone, giving off numerous branches, which anastomose freely, and form a fine reticulation around the gland cells, the larger branches running directly towards the central cavity, and forming loops by anastomosing with other similar vessels.

#### THE RECTAL PAPILLÆ.

The second set are the terminations of the main tracheæ. After giving off the lateral branches these run directly into the central cavity, where they become tortuous, and anastomose with each other, giving off comparatively few small vessels in proportion to their size, and forming a network which fills the central cavity, but none of their branches pierce its investing membrane anywhere. Fig. 9 represents the central cavity with its tracheæ, with a small portion of the lateral branches and their terminations amongst the glandular structure.

The gland cells are large—about 1-300th of an inch in diameter—and slightly angular by mutual pressure. Each contains a granular nucleus about one-third the diameter of the cell.

That these organs secrete uric acid seems probable both from their structure, and from the fact that uric acid is found in abundance below the recto-colic valve, and not above it.

I believe the central cavity is continuous with the visceral cavity, and that it affords a means of bringing the circulating fluid into almost immediate contact with the secreting cells, a fine structure-less membrane only being interposed—and still further I believe I am justified in asserting that the circulating fluid is expelled from, and a fresh supply is drawn into, the central cavity by a rhythmic muscular act.

In the female fly, the rectal papillæ lie fortunately between the second and third rings of the ovipositor when that organ is exserted, where it is sufficiently transparent to allow of the papillæ being seen during life. I have repeatedly observed a movement of the kind I have described. I believe this is the explanation of the radiating bands of muscle at the base of the papillæ. They probably open the central cavity, at the same time pressing upon the contents of the papilla, and, assisted by the muscular wall of the rectum, which contracts at the same instant, not only expel the contents of the central cavity, but also press the secreted fluid through the minute pores in the calyx into the cavity of the rectum. The central cavity is probably refilled by the elasticity of the calyx itself.

With regard to the urinary secretion, that which is passed by the insect when it first emerges from the pupa case, is a semi-solid

mass of nearly pure uric acid. That passed afterwards is a turbid fluid, sometimes almost clear, and very irritating when applied to any tender part of the skin. This fluid when acidulated with hydrochloric or nitric acid deposits an abundance of crystals of uric acid. I believe this acid is held in solution by ammonia. The excrement of the fly when heated over a lamp gives off a strong urinary smell.

No trace of these organs exists in the larva, which may be accounted for by its inactive mode of life. The bile tubes appear to be its only excretory organs.

# Section VI.—The Integument of the Thorax. PLATE V.

The integument of the thorax consists of no less than fifty-one pieces, some of which are extremely complex in form. The number is, however, much reduced if the smaller pieces connected with the articulation of the wings and halteres, the orifices of the respiratory organs, and the twelve forming the coxæ, are omitted. As these will be described in their respective places, and as five of the seventeen which remain are pairs, but twelve will need description here. These belong to four distinct segments, the first being the ventral and lateral plates of the fifth or last cephalic segment.

The ventral plate or sternum of the fifth segment forms a very remarkable organ, which I have named the cephalo-sternum (Plate V, Fig. 9). It consists of a saddle-shaped body with a pair of thin lobes directed forwards. The body is opaque and strengthened by ridges which support the lobes. These are thin and almost transparent; they are about 1-200th of an inch in diameter and are covered by a multitude of setze, about 1-600th of an inch in length, each having its base surrounded by a thickened ring, which gives the lobes a honeycombed appearance. In front of each lobe is a small leaf-like plate of opaque integument. The upper surface of the lobes is in apposition with a tuft of nerve filaments, which covers it, and which may be distinctly seen to terminate in nerve cells. The use of this organ is at present unknown, but it is probably an organ of special sense.

#### THE INTEGUMENT OF THE THORAX.

The lateral plates of this segment support the head. I have named them condyles (Plate V, Fig. 9). The condyle is very hard and opaque. When seen from beneath it is almost triangular, with the anterior angle prolonged into a rounded protuberance, which fits into the cup-shaped depression at the side of the occipital foramen. Seen from within it has an irregular form, due to the turning in of its edges. A process projects from its posterior external angle. Numerous muscles are inserted into it, which regulate the movements of the head.

The remainder of the thorax is composed of three segments. called the Pro-thorax, the Meso-thorax, and the Meta-thorax, They are all visible externally beneath, but above the whole pro-thorax and meta-thorax are concealed by the meso-thorax; laterally a small part of the pro-thorax and meta-thorax only is visible. Each consists of four plates, except the meso-thorax, in which the lateral plate is divided vertically into two. The inferior plates are called sterna, the lateral plates episterna, and the dorsal plates the terga, of their respective segments. The edges of each plate are turned in and form ridges and processes in the inside of the thorax, and the terga of both the meso- and meta-thorax are divided by similar ridges into four parts called respectively from before backward, the præ-scutum, the scutum, the scutellum, and the post-scutellum.

It is a fact worthy of remark that, although the tendency of the coalesence of segments is, that they unite first in the dorsal region, so in the dorsal region we find the greatest tendency for a single segment to become split up into several distinct parts. This is doubtless, in both cases, due to the fact that development commences in the embryo at the ventral surface, and the number of segments is there first determined by the number of distinct spots from which development proceeds. As the segments grow up towards the dorsum, they either split or coalesce with each other.

The back of the thorax is almost entirely formed by the tergum of the meso-thorax. That of the pro-thorax is reduced to little more than a mere rim around the superior part of the anterior

#### DESCRIPTION OF PLATE V.

Fig. 1. An anterior view of the thorax with the head removed, showing the cephalo-sternum and condyles in situ.  $\times$  8 diam.

Fig. 2. A vertical section of the thorax behind the wings, showing the manner in which the wings are united to the thorax, the meso-sternal ento-thorax, and para-pleura, together with the arrangement of the thoracic muscles. The non-striated longitudinal muscles are distinguished from the striated muscles by a difference in their tint, and the small space occupied by the viscera is well seen; it is marked by a blue tint.  $\times 8$  diam,

Fig. 3. The meso-thorax seen from above, showing its division into four distinct portions, as well as the insertion of the wings and winglets.  $\times$  6 diam.

Fig. 4. A posterior view of the thorax, the abdomen being removed showing the meta-thoracic tergum a, divided like the meso-thoracic tergum into four parts; b, is the ventral portion of the first abdominal segment; and c, c, represent the lateral portions of the meta-sternum. The winglets, halteres, posterior thoracic spiracles, and the posterior thoracic opening are shown.  $\times$  6 diam.

Fig. 5. A lateral view of the thorax, in which a is the meso-sternum, b, the anterior lateral plate of the meso-thorax, and c the side of the meta-sternum. The other portions will be easily understood by reference to the text.  $\times$  6 diam.

Fig. 6. A longitudinal vertical section of the thorax, showing the disposition of the main trachea, the ento-thorax of the meso and metasternum, and the great muscles of the back.  $\times$  6 diam.

Fig. 7. The under surface of the thorax, showing the four sterna, and the openings with which the coxæ are articulated.  $\times$  8 diam.

Fig. 8. The lower half of the thorax, seen from within, showing the four sterna with the ento-thoracic processes. a Represents the meso-sternum; b, b, the lateral plates of the meso-thorax; and c, c, portions of the meta-sternum.  $\times$  8 diam.

Fig. 9. The cephalo-sternum, condyles, and a portion of the pro-sternum, seen from within.  $\times$  15 diam.

Fig. 10. The pro-tergum, seen from within.  $\times$  15 diam.

Fig. 11. A portion of the flank, seen from within, showing the insertion of the wing and para-pleura, a, Part of the meso-sternum; b, episternum of meso-thorax; c, episternum of meta-thorax; d, side of scutellum; e, part of the dorsum of scutellum,  $\times$  8 diam.

Fig. 12. The insertion of the wing, from without, showing the wing, pivot and socket. *a*, The ampulla; *b*, support of the winglets; *c*, the sub-costal nervure, seen in section,  $\times$  25 diam,

Plate V





### THE INTEGUMENT OF THE THORAX.

thoracic opening, and that of the meta-thorax is invisible externally, except when the abdomen is very much depressed, being hidden under the post-scutellum of the meso-thorax.

The pro-sternum or sternum of the pro-thorax (Plate V, Figs. 1, 7, and 8,) is situated immediately behind the cephalo-sternum. It consists of a central portion and two cornua, which partially surround the anterior coxæ. The central portion is a long narrow plate, widest anteriorly ; it is grooved along the mesial line externally, and presents a slight ridge internally; posteriorly, it sends a narrow plate along the edge of the meso-sternum, and between it and the posterior edges of the coxæ on either side. This plate becomes broader externally to the coxa, and extends along the outer edge of its articulation, reaching the lower anterior margin of the anterior spiracle, where it unites with the lateral plate of the pro-thorax and terminates in a curved point in front of the articulation of the coxa, near its outer anterior angle, behind the condyle. A stout tooth springs from the outer margin of the aperture, near the anterior part of the opening, with which the coxa articulates ; it is hard and polished, fits into a hollow on the outer side of the coxa, and forms a point d'appui, upon which the leg moves.

The posterior extremity of the sternum internally bears a pair of processes, which are directed outwards upwards and forwards, and reach the lower margin of the anterior thoracic spiracles, where they bifurcate to surround those openings. I think it extremely probable that these processes are part of an undeveloped segment intermediate between the pro-thorax and meso-thorax.

The meso-sternum (Plate V, Figs. 2, 5 a, 7, and 8 a.) forms the greater part of the under surface of the thorax as well as part of the flank. It is marked inferiorly by a groove in the mesial line, and is deeply notched posteriorly for the intermediate coxæ. It bears very important internal processes; one, the ento-thorax of the meso-sternum, extends its whole length in the mesial line, and supports the great thoracic ganglion. This is Y-shaped when seen either in front or behind, but presents a large surface above, which lodges the ganglion; its lateral margins give insertion to muscles. Numerous muscles arise from and

Fig. 13. The rod borne by the ampulla, the free extremity of which fits into a concavity in front of the wing pivot.  $\times$  50 diam.

Fig. 14, The wing socket.  $\times$  50 diam.

Fig. 15. The valve, or epitreme, and peritreme of the meta-thoracic spiracle.  $\times$  25 diam

Fig. 16. The valve, or cpitreme, of the anterior thoracic spiracle,  $\times$  15 diam,

Fig. 17. The peritreme of the anterior thoracic spiracle.  $\times$  15 diam.

are inserted into the ento-thorax. Another process on each side is formed by the turning in of the posterior superior angle of the sternum; it gives origin to a number of muscles connected with the wings, and a broad muscular slip unites its inner edge with the external edge of the superior surface of the ento-thorax. I propose the term para-pleuron for this process.

The meta-sternum is very narrow beneath, the posterior being nearly approximated to the intermediate coxæ. It forms, however, a more considerable portion of the flank. Internally it bears a process in the mesial line, the meta-thoracic ento-thorax, which supports the great nerve trunk, the œsophagus, intestine, dorsal vessel, and salivary glands in their passage to the abdomen. This process is very similar to the ento-thorax of the meso-sternum, but is much narrower ; it almost meets that process anteriorly. A pair of strong ridges extend from it laterally along the anterior edges of the meta-sternum. It gives origin to several pairs of muscles.

The lateral plates of the pro-thorax are one on each side (Plate V Figs. 1, 5, and 8,); they are best seen internally, where their limits are defined by ridges. They are almost square, but the superior anterior angles unite them to the dorsal plate of this segment. Each is bounded inferiorly by the coxa, posteriorly by the anterior thoracic spiracle, and anteriorly by the condyle and anterior thoracic opening.

The lateral plates of the meso-thorax are two on each side, the larger is called the episternum, but the smaller, which is likewise posterior, does not appear to have received a name. I shall call it the posterior lateral plate of the meso-thorax,

The episternum (Plate V, Figs. 5 and 8 b) is almost square and very solid. Its superior posterior angle is prolonged into the thorax as anarrow process, from which the anterior muscles of the wing arise.

The posterior lateral plate (Plate V, Fig, 5) is deeply notched above for the insertion of the wing, but is otherwise nearly square; a small knob-like projection marks its anterior superior angle and is immediately in front of the insertion of the wing.

The lateral plates of the meta-thorax are one on each side. They are smaller than those of the meso-thorax, and are notched posteriorly for the insertion of the halteres; each is bounded below by the posterior thoracic spiracle, anteriorly by the posterior lateral plate of the mesothorax, above by the meta-thoracic tergum, and behind by the insertion of the halter and the first abdominal segment.

The tergum or dorsal plate of the pro-thorax (Plate V, Fig. 10) is reduced to a narrow ridge, which thickens the edge of the anterior thoracic opening and which gives off a pair of diverging processes posteriorly, for the origin of muscles, These are connected near their base by a thin trian-

### THOBACIC APPENDAGES.

gular membrane, in the free edge of which is a leaf-like thickening. Three curved ridges extend from the base of these processes upon the inner side of the præ-scutum of the meso-thorax, and give origin to muscles,

The meso-thoracic tergum is marked externally by four transverse lines, which divide it into four nearly equal portions. These are separated internally by ridges, which give origin to muscles as well as strengthen the whole structure ; that between the scutum and scutellum sends inwards a small pointed process near the origin of the wings, from which muscles arise for their movement. The lateral edges of the scutellum form a pair of thickened rods for the support of the articulation of the wing, and a loose fold of integument unites the scutellum to the lateral and dorsal plates of the meta-thorax and gives the chief freedom of motion to the whole dorsal region, as the scutum, præscutum, episternum and sternum of the meso-thorax are firmly soldered to each other, but are sufficiently elastic to allow of some movement in the folds between them. The cavity of the post-scutellum is entirely filled by a pair of air vessels (Plate V, Fig. 6).

The tergum of the meta-thorax is almost vertical in its direction. It forms the posterior wall of the thorax, and it is distinctly divided into four parts by ridges corresponding to the same parts of the meso-thoracic tergum; two of these, however, the scutellum and post-scutellum, only appear internally, the first abdominal segment arising apparently from the junction of the scutum and scutellum.

# Section VII.—The Thoracic Appendages. PLATE I.; PLATE V., FIGS 12—14; PLATE VI.

The wings consist, as has been stated above, of a double membrane.\* This is kept extended by a system of nervures, which chiefly arise from two primary nervures. An anterior or costal, which runs along the anterior margin of the wing to its extremity, and a posterior or sub-costal, which arises in common with the former, and runs for a short distance parallel to it, and then splits up into four trunks, which all terminate by joining the costal nervure. Another set of

\* Page 18.

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nervures arise in a fold of the wing posterior to the sub-costal nervure, which all become very fine, and are ultimately lost near the posterior edge of the wing, which is not guarded by any nervure. These are not connected with the cavity of the thorax by any open canal, like the costal and sub-costal nervures; but the two systems communicate by a short transverse trunk from the posterior branch of the sub-costal near the middle of the wing.

The costal nervure is protected at its origin by a small scale or epaulet called the pterogodium, fringed with hairs; beneath this is a broad scalelike fold, which forms the basal joint of the costal nervure, and which is

### DESCRIPTION OF PLATE VI.

#### The Development and Appendages of the Thorax,

Fig. 1. The nerve centres of the larva, with the imaginal discs of the optic and autennal segment-, and of the four anterior legs firmly attached to them.  $\times$  30 diam.

Fig. 2. The lateral tracheal vessel of the larva, showing its inner and outer coat, with the imaginal discs of the wing, halter, and posterior leg firmly attached to it.  $\times$  30 diam.

Fig. 3. The first stage of unfolding of the imaginal discs of the anterior pair of legs, showing their capsules.  $\times$  15 diam.

Fig. 4. One of the anterior leg discs unfolded and considerably developed; about the third day of the pupa state.  $\times$  30 diam.

Fig. 5. The same, at the end of the first week, with the leg of the fly seen within in process of development.  $\times$  20 diam.

Fig. 6. The intermediate leg of the fly.  $\times$  10 diam.

Fig. 7. The tibia of the same, with muscles attached.  $\times$  10 diam.

Fig. 8. The first tarsal joint, with its muscles.  $\times$  10 diam

Fig. 9. The last three tarsal joints.  $\times$  20 diam.

Fig. 10. The last tarsal joint, with its long apodéme and muscle, arising from the femur.  $\times$  10 diam.

Fig. 11. The pulvilli and claws.  $\times$  75 diam.

Plate VI





#### THOBACIC APPENDAGES.

connected closely by a membrane with the scutellum above and loosely with the flank below; it is covered with fine hairs. The second joint of the costal nervure is united to the first by membrane. It is an elongated scale, with its anterior edge curved downwards, so that the anterior edge of the wing appears to possess considerable thickness. The cavity of this scale is very narrow, and, I believe, becomes obliterated entircly in the adult insect. This scale bears a large number of short thick hairs. The costal nervure is continued directly backwards along the margin of the wing from the posterior extremity of this scale. There is, however, the indicacation of a joint between them. The nervure is set with strong spine-like hairs, and its canal is entirely obliterated by the fibrillation of the mesoderm.

The sub-costal nervure, unlike the costal, remains tubular during the whole life of the insect, and contains a nerve and tracheal vessel in their passage to certain structures, which may be observed on the nervure.

The sub-costal is almost cylindrical, except at its origin, where it spreads out into a broad scale, which is closely united to the basal scale of the costal nervure. A strong tooth projects from its underside near to its origin, which I shall call the wing-pivot. This consists of a clear amber-coloured, excessively hard process of chitine, exactly similar to that which forms the extremity of the mandibles in some insects. Its extremity fits into a hollow, in a similar process, which is supported by the flank, and which is shaped something like an inverted molar tooth (Plate V., figs. 12 and 14).

The organs on the sub-costal nervure, to which the nerve is distributed, are several groups of transparent spots, exactly similar to those on the base of the halteres. These were first pointed out by Dr. Braxton Hicks,\* and appear very constant in all insects except the Orthoptera and the Colcoptera, where their presence needs confirmation, as they are very different from the double refracting circular bodies so common in their elytra, with which they appear, however, to have been confounded. These organs will be described at length in Section XVIII. I have also traced filaments of the nerve to the bulbs of the hairs, which are situated on an enlargement of the posterior branch of the sub-costal.

Behind the origin of the sub-costal nervure is a thickened chitinous fold, which bears the winglets (plate V., fig. 12 b). It is closely connected above with the sub-costal nervure, and beneath with the rod which forms the interior margin of the scutellum. Its external process bears the winglets which are attached to its margin. When the wing is at rest, this

\* Linn. Soc. Trans., 1856-57.

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process is directed forwards, as is represented in the plate, but it is capable of revolving like a hinge, so that when the wing is open this process is directed outwards.

Beneath the last is an irregular-shaped piece of chitine, completing the outer circle of the wing joint, and uniting with the anterior superior angle of the posterior lateral plate of the meso-thorax. This latter bears a protuberance (Plate V., fig. 12 a), filled internally with muscle, which I shall call the ampulla.

The ampulla hangs over the anterior portion of the wing joint. Its posterior edge bears an irregular ring of chitine beneath the integument, which supports three very remarkable processes; the centre of this ring is occupied by a loose puckered membrane.

The most important of these processes is shaped like an inverted molartooth—(Plate V., figs. 12 & 14); it supports the wing pivot in its cavity, and is probably the joint upon which the wing swings, when rapidly vibrating. It is excessively hard and semi-transparent, like the wing pivot, —I shall call it the wing-s ocket.

In front of the wing-socket is a flattened rod, broadest at its free extremity, and slightly curved—(Plate V. figs. 12 & 13). Its free extremity is covered with a soft elastic substance, which easily separates from the rod itself, which is as hard as the wing-socket. Its free extremity fits a small cavity in the anterior part of the base of the tooth beneath the subcostal nervure, or wing-pivot. Its function may be to keep the wing back whilst vibrating, or even to stop its vibrations, a view indicated by its soft elastic extremity. The third and last process appears to be rudimentary, it consists of a single hardened tooth directed backwards; I think it may support the wing-pivot in some positions, but have not been able to make out its use.

The muscles attached to these parts are very numerous, and are most of them furnished with fine tendons; each muscle consists of a few fibres. They arise from the several internal processes already indicated, but at present the exact origin and insertion of each has not been made out. Shortly, it may be said that every separate piece is furnished with at least two muscles, an extensor and flexor, or an elevator and depressor as the case may be.

The legs consist of several tubular articulations, the names of which have already been given,\* but the three pairs differ somewhat, especially as to the coxæ.

\* Page 19.

#### TRORACIC APPENDAGES.

The anterior coxæ are the largest ; each consists of a flattened, almost quadrilateral, tubular joint, loosely united by membrane to the pro-sternum. A depression on its outer side lodges a strong tooth, borne by the edge of the pro-sternum, upon which the whole limb moves, so that the joint possesses a freedom of motion almost equal to that of a ball and socket. Another smaller triangular plate is interposed between the coxa and the anterior part of the sternum on the inner side of the limb. This is probably the representative of the basal joint of the coxa, whilst the larger part of the joint corresponds to the second article of the other coxæ.

The femur is articulated with the coxa by a hinge allowing of movement in only one direction; all lateral motion being prevented by the edges of the coxa overlapping the femur, and forming a groove, in which it moves. A small accessory plate, closely united to the femur, protects the under side of the joint.

The intermediate coxæ each consist of a basal segment, which is somewhat boat-shaped, but open both above and below. It is flattened anteriorly, and pointed externally. Its anterior edge fits against the posterior edge of the meso-sternum. A stout tooth, but not so large as that which supports the anterior coxa, fits against its inner anterior angle. It projects from the posterior edge of the meso-sternum, near the mesial line. The joint between this part of the coxa and the mesosternum is a hinge joint, moving on its posterior edge, and giving the limb a motion in an antero-posterior direction.

The second joint of the intermediate coxa is short, and almost conical. It is loosely connected with the last, and has a hinge-like motion upon its posterior and inner edge, which gives the limb a considerable lateral play.

The posterior coxæ differ from the intermediate, in the first joint being more nearly round, and in the absence of any well-marked tooth at the inner and posterior part of the meta-sternum. A very small tooth exists, however, externally to the limb at the edge of the meta-sternum. These teeth, both in the intermediate and posterior limbs, seem to act rather as checks to the movement of the limb, preventing the thoracic muscles from drawing the coxa into the interior of the thorax, than as pivots, upon which the coxæ move, like those of the anterior limbs.

The joints between the coxæ and femora in the posterior and intermediate limbs, resemble the same in the anterior legs. The articulations between the femora and tibiæ allow of no lateral motion, the femur being grooved vertically for the reception of the tibia. The tarsal joints allow of slight lateral motion, the distal extremity of each being hollowed beneath into a cone-like cavity, which receives the narrow proximal end of the next. A similar joint exists between the proximal tarsal articulus and the tibia,

only very little lateral movement is allowed, from the manner in which the muscles are inserted into it.

The muscles which move the coxæ and femora arise from the back, and form the vertical groups of muscles, which occupy the lateral regions of the thorax. A pair are inserted by fleshy insertions into each portion of the coxa, and another pair terminate in tendons, and are inserted into the proximal extremity of each femur, one into its upper or outer, and one into its lower or inner margin, the former being a flexor and the latter an extensor of the limb. The tendons of the anterior femoral muscles receive fleshy slips, which arise within the anterior coxæ, and are inserted into them in a bipenniform manner.

Each of the other joints, except those of the tarsus, gives rise to a pair of bipenniform muscles, a flexor and extensor of the succeeding joint. The muscle, which moves the terminal joint of the tarsus, arises in the upper part of the femur, and is connected with the last tarsal joint by a long threadlike apodéme. The apodéme is connected with the proximal extremity of each tarsal joint by a membranous slip, and terminates in a triangular plate, which bears the pulvilli and claws. This plate is grooved below by a number of parallel grooves on either side of the mesial line. These are seen very frequently in the feet of insects. It terminates in a long blunt spine, and supports the pulvilli beneath, as well as the claws above.

The last four tarsal joints are occupied, as has been already stated,\* by a sac, which secretes a viscid fluid. As I have only succeeded in seeing this sac in the manner already indicated, I cannot say whether it is single or double; neither can I tell whether the fluid secreted by it is conveyed into the pulvilli by ducts or by an opening in the neck of the sac, or whether it passes into it simply by transudation. The great delicacy of the secreting sac and the opacity of the tarsus renders it exceedingly difficult, if not impossible, to make out these details in the fly.

### Section VIII.—The Abdominal Segments.

The abdominal segments are far less complicated than those of the thorax. They are nine in number, but the last four are modified to form the sexual organs, these will be described in their proper places.

\* Page 19. † Page 104.

### THE RESPIRATORY ORGANS.

The five anterior abdominal rings each consists of a narrow ventral plate loosely united by membrane to a dorsal arch, which encircles more than four-fifths of the abdomen, and which is perforated beneath by a pair of small round spiracles.

The first abdominal segment is reduced above and laterally to an exceedingly narrow ring; its ventral plate is well marked but very short, although it is wider than the other ventral plates. The next four abdominal segments enclose the greater portion of the abdominal The first ring is contracted in front, the second is equally cavity. contracted both in front and behind, whilst the two posterior rings form the conical apex of the abdomen. The ventral plates of these segments are longest from before backward; and the last in the male is deeply divided behind. The membrane between the ventral and dorsal plates is sufficiently loose to allow of considerable extension of the abdomen by the separation of the plates, but they are united by a series of flat muscular bands which cover the whole inner surface of the abdomen. These may be divided into three sets-ventral, dorsal, and transverse. The ventral muscles are the largest and most conspicuous. They form pyramidal bundles on each side of the mesial line. They arise from the anterior part of each ventral plate near the mesial line, and are inserted into the anterior border of the next ventral plate, by an insertion rather broader than their origin. A few fibres pass occasionally from one muscle to join the insertion of the next. The transverse muscles are narrow muscular bands, which arise from the sides of the ventral plates at the junction of their middle and outer thirds, and are inserted into the adjacent edges of the dorsal arches. The dorsal muscles arise from the anterior part of each dorsal arch below, but near their posterior edges above, and are inserted into the anterior edge of the next dorsal arch. All the muscles are best seen by hardening the part in spirit or chromic acid. This renders them opaque, so that they may be easily observed by viewing the abdominal integument by reflected light.

### Section IX.—The Respiratory Organs.

PLATE I., PLATE V., FIGS 6 AND 15-17, AND PLATE IX., FIG. 4.

The spiracles or external openings of the respiratory organs are ten in number on each side of the male, and eight in the female.

The anterior thoracic spiracle (plate  $\nabla$ ., fig. 17) is oval and narrowest above. Its margin consists of a thickened ring chiefly visible internally, and formed by the extremities of the process already described as extending from the posterior extremity of the central portion of the pro-sternum to the spiracle.

The anterior spiracle is situated between the pro-thorax and meso-thorax, but the meso-thoracic tergum reaches over its superior margin, and joins the pro-thorax in front of the spiracle; beneath it is entirely bounded by the pro-thorax. The edge of the spiracle is continued as a thin semi-lunar fold, which reduces the opening to a mere slit. This is strengthened by chitinous arborescent nervures, which project beyond its free edge, so as to fringe it with a delicate fringe of sharp spicules. I shall call it the peritreme, although in the posterior thoracic spiracle the same structure forms a pair of leaf-like valves.

Close behind the peritreme is the true valve by which the aperture is closed This resembles a pair of callipers jointed below, but the two sides shut against each other like the leaves of a book. I shall call this structure the epitreme (plate  $\nabla$ ., fig. 16). It is closely united to the wall of the tracheal vessel, and is probably developed in its inner layer or that which corresponds to the protoderm. By breaking away a small portion of the peritreme of the anterior spiracle of the living fly, the epitreme may be observed opening and closing regularly with each act of respiration. As has been already observed, when a fly is held by the wings it makes regular efforts with its legs; during these the peritreme remains closed, but may be observed to open as soon as the effort ceases.

The peritreme of the anterior spiracle is opened and closed

#### THE NERVOUS SYSTEM.

by a small muscle, which arises from the margin of the spiracle below, and is inserted into a pair of thin plates, close to the hinge of the peritreme. The structure of the posterior thoracic spiracles differs only in detail from that of the anterior.

The posterior thoracic spiracle may be said to be triangular, with rounded angles; its superior border is longest and straight, the other sides are slightly curved, the posterior edge is shortest. It is surrounded internally by a deep ridge, derived from the posterior margin of the meta-sternum, which is especially marked at the posterior inferior angle of the spiracle.

The pseudo-valves, or peritreme, consist of a pair of valve-like plates, a small posterior, and a large anterior valve. These are attached beneath to the meta-sternum, which forms the inferior boundaries of the spiracle; the upper margin of which is formed of the lateral plate of the metathorax, and this is so deeply notched behind, that the halter arises quite close to the posterior superior angle of the spiracle. The pseudovalves are strengthened by arborescent nervures similar to those of the peritreme of the anterior spiracle.

The valve or epitreme arises from the posterior inferior border of the spiracle: its hinge resembles that of the epitreme of the anterior spiracle, except that the plates into which the muscle is inserted are beneath the hinge. Its action has not been observed during life, owing to its depth from the surface being greater than that of the epitreme in the anterior spiracle. It undoubtedly entirely closes the opening, but it is uncertain whether its opening and closing is synchronous with that of the anterior epitreme.

The main trachea of the thorax extends on each side from the anterior to the posterior thoracic spiracle, lying close to the thoracic viscera. It sends a large branch which curves inwards and forwards into the head, and another smaller branch into the abdomen. This latter swells ont on each side into the great abdominal pulmonary sac. More properly, perhaps, the anterior and posterior portions should be called continuations of the lateral tracheæ and the portions uniting it with the spiracles should be looked upon as branches. A large trunk from the posterior thoracic spiracle follows the wall of the thorax upwards and inwards; it sends a large branch forwards in the mesial line between the muscles and the back. This gradually becomes narrower and supplies the dorsal muscles, and sends a prolongation backwards which fills the whole cavity of the post-scutellum.—(Plate I. & Plate V. fig. 6).

A number of small sacculi, connected with each other in a chain, extend

on each side from the main trachea near the anterior thoracic spiracle, to the same vessel near the posterior thoracic spiracle. These lie between the lateral thoracic muscles which they partially supply—they also send branches to the legs.

The cephalic branches of the lateral tracheæ pass into the head and expand into sacs which envelope the posterior and lateral portions of the cephalic ganglion. Each of these sends a large branch forward to the insertion of the antennæ, which is continued along the side of the pharyux to the proboscis; and numerous offsets to the compound eyes, which they almost surround.

Another and smaller portion of the cephalic branch of the lateral thoracic trunk passes over the cephalic ganglion and unites with its fellow in the mesial line just behind the nerve to the ocelli. It sends off several lateral offsets to the lateral portions of the cephalic ganglia, and supplies the ocelli.

The abdominal pulmonary sacs are connected by a narrow vessel with the posterior extremity of the lateral thoracic trunk. They are very large and spherical, occupying almost the whole base of the abdomen. Each gives off several sets of vessels, kept open by a spiral fibre to the abdominal viscera and dorsal vessel. With this exception, all the tracheæ already described are membranous in the adult insect.

The abdominal spiracles are small round pores, about 1-200th of an inch in diameter—although they vary considerably in size—in the underside of the dorsal arches. There are none to the first segment, the dorsal arch being rudimentary. The next four have each a pair; but the sixth abdominal—or first segment of the generative organs — has two pairs in the female, one above the other, and only one in the male. The remaining segments have none in the female, but the seventh has two pairs, and the eighth a single pair, in the male.

The peritreme of the abdominal spiracles is a mere thickened rim, with a number of minute spiculæ projecting from its margin. The epitreme is situated about 1-150th of an inch within the spiracle, and is connected with the peritreme by a short unbranched tracheal tube, with a few thread-like rings

#### THE DORSAL VESSEL.

in its wall. The epitreme consists of a ring more or less hardened on one side, from which a kind of handle projects. This handle is connected with the ring differently on its two sides, the junction being vertical on one side and horizontal on the other (Plate IX., fig. 4). A short muscle arises from the peritreme, and is inserted into the handle of the epitreme. The spiracle is closed by depressing the handle, which folds the vertical against the horizontal half of the ring. Immediately within the epitreme the trachea swells out, and gives off numerous large branches, each one as large or larger than the trunk between the epitreme and the peritreme.

### Section X .- The Dorsal Vessel.

### PLATE IX., FIG. 1.

The dorsal vessel of the fly is perhaps the most difficult organ in the insect to make out thoroughly. Its walls consist of three coats at least; an external muscular, an intermediate membranous, and an internal elastic coat. The external and middle coats seem to form only a loose investment around the elastic tunic in the abdomen, and after death when the vessel is empty they appear as a semi-transparent fusiform flattened band beneath the integument. They seem to be stretched laterally by the tracheal vessels which supply them, and probably also by a thin membranous expansion which connects them with the abdominal parietes. The muscular fibres are striated; and the majority, if not all, are longitudinal. I am inclined to regard this portion of the organ as homologous to the lateral wings of the dorsal vessel of the cockchafer.

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The internal or elastic coat is constricted at intervals, forming five chambers, with a valvular fold between each. The three posterior chambers are very narrow, slightly enlarged at their anterior extremities; but the two anterior form a considerable dilatation. Each has a pair of small lateral openings protected internally by a valvular fold. The elasticity of this coat causes the vessel to curl up when detached from the abdominal wall; it probably keeps the chambers open\* during life, whilst they are emptied successively by the contraction of the muscles which surround them. So that the action of the vessel is analogous to that of Dr. Richardson's æther spray apparatus. The contraction of the whole length of the muscular coat is not simultaneous, but takes place by a series of undulations commencing at its posterior extremity.

The anterior abdominal chamber is prolonged anteriorly as a tubular vessel, which lies above the chyle stomach and beneath the great dorsal thoracic muscles. This vessel enters the head above the œsophagus, and ends by branching into six or eight minute tubes, which terminate in open mouths in the cephalic cavity. The muscular wall of the dorsal vessel in the abdomen is continued in the thoracic portion of the vessel and its terminal branches; but the elastic coat is either absent or very little developed.

The development of the dorsal vessel has not hitherto been worked out. The difficulties of the necessary observations are very great, from its great transparency and elasticity. It is

<sup>\*</sup> This is the only theory I can suggest to account for the dilatation of the dorsal vessel, since the influx of fluid can have no effect in dilating the chambers, as in animals having a closed circulation. I think it probable that the wings of the dorsal vessel of the cockchafer enclose an elastic tube exactly as the muscular tube encloses the elastic one in the fly, except that their direction is transverse instead of longitudinal.

most easily observed in the living insect when it first emerges from the pupa. When removed from the abdomen the folds of the elastic coat are easily obliterated, unless it is first hardened in a solution of chromic acid.

### Section XI.—The Nervous System.

### PLATE VI., FIG. 1, AND PLATE VII., FIGS. 1-4 AND 10.

The parts of which the nervous system is composed have already been indicated.\* The cephalic nerve centre will be best described by describing its component ganglia. These are three pairs, which I shall name the central or antennal, the anterior or cerebroid, and the lateral or optic ganglia.

The great thoracic nerve cord forms the lowest portion of the cephalic nerve centre, and when seen from beneath appears as a somewhat lozenge-shaped flat surface, from the anterior portion of which the great nerves of the probocis arise. These appear to be chiefly composed of fibres from this cord. A pair of crura arise from the upper side of the thoracic cord, and diverge to allow the cesophagus to pass between them; these enter the cephalic nerve centre where their fibres spread out, and connect the different ganglia of which it is composed. The tracing of these is exceedingly difficult, but I believe I have clearly made out, that a large bundle extends to each optic ganglion, that another set chiefly run up the back of the central ganglia, whilst others accompany the cesophagus, and appear anteriorly as a pair of small nerves, upon which the

\* Page 13.

ganglia of the proboscis are situated. I shall call these the cesophageal nerves.

The central ganglia form an ovate mass pierced by the cesophagus, and supported below by the expanded extremity and crura of the thoracic nerve trunk. A slight groove above

#### DESCRIPTION OF PLATE VII.

Fig. 1. The entire ventral cord and the cephalic and thoracic ganglia. The great splachnic ganglion and a few sympathetic nerves are represented as they would appear if it were possible to detach them from the viscera, to show their connection with the moto-sensory nerves.  $\times$  15 diam.

Fig. 2. A vertical section through the middle of the cephalic ganglion, showing the cesophagus, the nerves of the antennæ and proboscis at their origin, and a portion of the cephalo-thoracic ventral cord, and the cerebroid ganglion of the right side with its crus : to show the relations of these parts.  $\times$  30 diam.

Fig. 3. The anterior termination of the great cephalo-thoracic ventral cord, showing the crura of the optic ganglia and nerves to the proboscis; the pharyngeal and oral ganglia are also represented.  $\times$  30 diam.

Fig. 4. The cerebroid ganglia, isolated.  $\times$  100 diam.

Fig. 5. A portion of the interior of the great eyes, showing from above downwards, the following parts : a portion of the compound cornea, the cones and rods, with nuclei imbedded in their inner extremities, the common retina, the clear optic nerve, and the optic zone with its tracheal vessels.  $\times$  150 diam.

Fig. 6. Inner extremities of rods with their nuclei; a plexus of tracheal vessels and the choroid pigment is seen between the rods.  $\times$  500 diam.

Fig. 7. A cone detached, with the outer extremity of its rod and a single facet of the cornea, showing the structure of the rod, disposition of pigment, and nuclei in the pigment layer of the cone.  $\times$  600 diam.

Fig. 8. One of the ocelli, showing the cornea, choroid, and plexus of tracheal vessels.  $\times$  200 diam.

Fig. 9. The cornea of one of the ocelli, seen in profile.  $\times$  200 diam.

Fig. 10. Ultimate nerve loops of the sympathetic nerves of the ovary.  $\times$  500 diam.





### THE NERVOUS SYSTEM.

indicates the division of the two ganglia; the nerve to the ocelli appears to arise from this groove, but has more probably a deep origin from the optic ganglion. Anteriorly, the central ganglia are hollowed out for the reception of the anterior ganglia; beneath this hollow they give off the great antennal nerves. I have observed slight convolutions situated in the interior of the central ganglia, on making a section through them.

The anterior or cerebroid ganglia (Plate VII., figs. 2 and 4) are very remarkable nerve centres, supported on a pair of round peduncles, deeply convoluted and united by a well marked commissure in the mesial line. These give off no nerves, and their peduncles seem to arise partly in the substance of the central ganglia, and partly from the thoracic nerve trunk. They are best seen by making vertical sections of the whole cephalic nerve centre after hardening in spirit; but may be seen very frequently by carefully compressing the hardened nerve centre between the slide and thin glass. Their demonstration is not very easy without great practice, owing to their being imbedded in the central ganglia.

The lateral ganglia form an ovate mass on either side of the central ganglia. They differ in no way apparently, as far as structure is concerned, from the other ganglia; but they are covered externally by a thick layer of nerve cells, very largely supplied with tracheal vessels, which form long loops parallel to each other. They give origin externally to the nerves of the compound eyes.

The cephalic nerve centre is supplied by very minute tracheal vessels. These arise from the great tracheal sacs, which almost entirely invest it.

The cesophageal nerves appear close to the under side of the

cesophagus, where it emerges from the cephalic nerve centre. Near the posterior extremity of the pharynx, each gives off a branch, and these uniting, bear a small ganglion between them, which I shall name the pharyngeal ganglion. Although I believe it may possibly correspond to the frontal ganglion of Lyonet, as I am not sure, it seems better to name it after the organ against which it is situated. The remainder of the cesophageal nerves is distributed to the muscles of the pharynx.

A pair of small nerves arise from the pharyngeal ganglion, and run beneath the muscles of the salivary valve, which they supply; a little anterior to the valve they again unite, and bear a ganglion, which sends filaments to the mouth,—I shall call it the oral ganglion.

The great nerves to the proboscis arise from beneath the central portion of the cephalic nerve centre. Near the posterior part of the first joint of the proboscis they divide into three large trunks, which supply the palpi, the muscles of the proboscis, except those of the pharynx, and the great lobes of the proboscis, ending in loops upon the hair bulbs, and supplying the nipple-shaped processes upon the surface of the lobes.

The nerves to the antennæ, ocelli, and great eyes, will be described with those organs.

The thoracic nerve centre is supported by the meso-sternal ento-thorax, and consists of four pairs of large ganglia, of which the second are the largest, and the fourth the smallest.

Externally, the thoracic nerve centre appears to consist chiefly of nerve fibres, having a longitudinal direction. These form a kind of envelope around the several ganglia, which they connect with each other. The ganglia consist chiefly of nerve cells, and are largely supplied with tracheal vessels.

#### THE NERVOUS SYSTEM.

The nerves which are given off from the thoracic nerve centre, appear to arise chiefly from its external or fibrons layer, hence it is difficult to determine precisely to which ganglion they belong. Three large and two small pairs arise from the upper, and an equal number from the under surface of the nerve centre.

The first large pair arise from the upper surface of the first pair of ganglia; they are distributed to the muscles of the pro-thorax, and probably also, to the integument.\* A branch of this nerve ends in nerve cells upon the thin lobes of the cephalo-sternum.

The second pair arise with the last, and apparently supply the muscles and integument of the pro-thorax.

The third pair arise beneath the nerve centre, apparently between the first and second ganglia, chiefly from the first; they are especially distributed to the anterior pair of legs. They supply the muscles; a large terminal branch bifurcates in the tarsus, and supplies the integument of the tarsus, the pulvilli and claws.

The fourth pair are very large; they arise from the upper surface between the first and second ganglia. They chiefly supply the muscles of the meso-thorax; they probably also supply the integument. A small branch enters the subcostal nervure of the wing, and is distributed to certain special structures described in Section XIII.

The fifth pair arise from the under surface of the second pair of ganglia; they are distributed to the intermediate legs. Their distribution is similar to that of the third pair.

The sixth are a small pair from the upper surface of the second ganglia; they are probably chiefly motor, and accessory to the fourth.

The seventh pair are distributed to the halteres; they arise from above the junction of the second and third ganglia.

The eighth are probably merely an offset of the ninth; they are a small pair like the second and sixth. I am not certain, whether these small

\* In giving the distribution of these nerves, I have attempted to give an approximate idea; I have only traced the larger branches, and even that is a most minute and difficult dissection. Many which appear to end in muscles may pierce them, whence it is almost impossible to be quite certain of their distribution.

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nerves are sensory, or motor, or both; they seem to be lost amongst the muscles.

The ninth arise beneath, between the third and fourth ganglia, chiefly from the third; they supply the posterior legs, and are distributed similarly to the third and fifth nerves.

The tenth pair are small cords, which arise from the fourth pair of ganglia behind; they enter the abdomen, and are apparently chiefly lost amongst the cells and fibres of the sympathetic plexus. I have distinctly traced a connection between the two systems at this point.

The ventral cord is continued from the posterior extremity of the thoracic nerve centre; its fibres may be traced passing backwards from the surface of the latter. It is the great abdominal nerve, and gives off a pair of nerves for each segment; it terminates in numerous branches to the generative organs. No ganglionic swellings exist in this nerve.

The sympathetic or visceral system of nerves has three large and a multitude of small nerve centres.

The largest, which I shall call the great splanchnic, should probably be considered as a pair of ganglia. It is situated in the posterior opening of the thorax, and is covered beneath by a layer of orange brown hexagonal pigment cells. It is largely supplied with minute tracheal vessels, which form a loose network, between the meshes of which, a vast number of nerve cells and fibres lie. The great splanchnic seems to be connected with all the visceral ganglia, and to send branches over the surface of all the viscera.

A pair of large ganglia are spread out upon the surface of the crura, which connect the cosophagus and lateral lobes of the sucking stomach, one on each side of that organ. These are closely connected with the great splanchnic ganglion.

Numerous small ganglia abound upon the viscera, and

#### THE NERVOUS SYSTEM.

the whole are connected by meshes of fibres, which appear like strings of clear gelatinous looking nerve substance, flattened and spread out in places, apparently without any neurilemma (Plate VII., fig. 10). These nerves are especially abundant around the ovaries and testes.

In the larva, all the nerve centres are concentrated in the anterior segments. They consist of a pair of hemispherical ganglia above the œsophagus, supra-œsophageal; and a large flattened nerve centre, composed of a series, probably of twelve pairs of ganglia, beneath the œsophagus, sub-œsophageal (Plate VI., fig. 1).

The supra-œsophageal ganglia are connected by a pair of thick crura with the sub-œsophageal nerve centre. These crura become considerably lengthened at the commencement of the pupa state, and ultimately unite posteriorly, and form the great cephalo-thoracic trunk, uniting the cephalic and thoracic ganglia.

The supra-œsophageal ganglia of the larva seem to correspond to the lateral or optic ganglia of the imago. They give off a pair of nerves to the rudimentary sensory organs of the maggot; but I have been able to detect no commissure between these ganglia, above the œsophagus. About the third day of the pupa state a pair of small oval ganglia appear, uniting the supra-œsophageal ganglia; these are the rudimentary antennal or central ganglia of the imago. They seem to be developed in the crura of the supra-œsophageal ganglia, and they may exist in an extremely rudimentary condition in the larva, although I have entirely failed to detect them. The subcesophageal nerve centre consists of a series of ganglia, closely united to each other, which give off twelve pair of nerves to the twelve posterior segments of the larva. In the pupa it is G 2

gradually separated from the supra-œsophageal ganglia, by the development of the cephalo-thoracic nerve trunk from the crura of the latter. It still supplies the twelve posterior segments of the imago, although the number of ganglia is reduced to four pairs, either by the suppression, or more probably by the coalescence, of several.

The nerve centres of the larva are surrounded by the imaginal discs, from which the head and part of the thorax of the imago is developed.

# Section XII .- The Compound Eyes.

### PLATE VII., FIGS. 5-7, AND PLATE VIII., FIGS. 1 & 2,

The compound eyes consist of a compound cornea, beneath which are the rods and cones. These are connected with the nerve centre through the medium of nerve cells and fibres.

The compound cornea is covered by a layer of protoderm, which retains the form of the lenses beneath, when these are dissolved out with a solution of caustic potash. The lenses (Plate VIII., fig. 1), are bi-convex, consist of a transparent substance, and are united to each other by a flat frame-work of the same material. In fact, the compound cornea ought properly to be considered as a single piece, sculptured, as it were, into numerous lenses The diameter of each lens is about 1-1000th of  $a_{14}$  inch. The interlenticular spaces are generally hexagonal frames, but some near the edge of the cye are almost square.

#### THE COMPOUND ETES.

Beneath the cornea are the cones (Plate VII., figs. 5, & 7) These are clear conical transparent bodies, about 1-700th of an inch in length, which are surrounded by a membrane coloured with bright red pigment, and containing nuclei. A clear basement membrane exists between the substance of the cones and the pigment membrane, and the latter is probably formed entirely by the coalescence of pigment cells. The inner surface of the lenses of the cornea and the bases of the cones correspond, each lens having its own cone.

The rods (Plate VII., figs 5 and 6), by which the cones are continued to the nerve centre, are cylindrical, and connect the apices of the cones with a layer of nerve cells beneath. They are separated from each other by considerable spaces, traversed by tracheal vessels, and filled with red pigment. Each rod is nearly 1-100th of an inch in length.

The rods consist of an external or cortical substance, which forms the greater part of their thickness. A clear axis cylinder, continuous with the axis of the cone, may be observed. A third layer of transparent material appears to be interposed between the axis cylinder and the cortical part of the rods, and to extend as a thin layer into the cones between the pigmentary and transparent portions of those bodies. At the apex of each cone and around the outer extremity of the corresponding rod is a thickened ring of pigment, the use of which is unknown. A nucleus-like body, refracting light strongly and coloured like the pigment, is imbedded in the inner extremity of each rod. It is best seen by hardening the part in a solution of chromic acid. The inner extremities of the rods are imbedded in a thin layer of nerve cells, which I shall call the common retina.

Little can be said concerning the uses of the parts above described. I think it not improbable, that the hollow cylinders

intermediate between the cortical and axis cylinders of the rods are nerve tissue, expanding into retine between the pigmentary and transparent portions of the cones, and connecting these partial retine with the common retina beneath. On the other hand it is, perhaps, the common retina which receives the picture, the whole of the rods and cones being

#### DESCRIPTION OF PLATE VIII.

Fig. 1. A small portion of the compound cornea. × 300 diam.

Fig. 2. The epineuron of the right eye, seen from within, with part of its muscle.  $\times$  25 diam.

Fig. 3. The haltere, seen from above.  $\times$  100 diam.

Fig. 4. A portion of one of the cylinders, from the base of the haltere.  $\times$  500 diam.

Fig. 5. A portion of one of the dome segments, from the base of the halteres.  $\times$  500 diam.

Fig. 6. Section of one of the cylinders, showing the otoconia and nerve c-lls and fibres beneath its ridges.  $\times$  500 diam.

Fig. 7. A small portion of the subcostal nervure, showing part of a row of wing o gans.  $\times$  300 diam.

Fig. 8. The antenna of the right side.  $\times$  50 diam.

Fig. 9. First joint of the same.  $\times$  75 diam.

Fig. 10. Second joint of the same.  $\times$  75.

Fig. 11. Diagramatic representation of a compound sacculus, from the third joint of the antenna, seen from above.

Fig. 12. Diagramatic section of the wall of the third joint of the antenna, showing one of the compound and two simple sacculi-

Fig. 13. Terminal branches of antennal nerve, from the third joint of the antenna.  $\times$  about 500 diam.

Fig. 14. A small portion of the frontal sac, showing its papillæ  $\times$  750 diam.

Fig. 15. A small portion of the maxillary palpus, showing its saccular organs.  $\times$  200 diam,

Fig. 16. One blade of the cephalo-sternum.  $\times$  300 diam.

Plate VIII




#### THE COMPOUND EYES.

concerned in its formation. At present nothing certain can be said on the subject, although I incline entirely to the former view.

The cones and rods form a layer rather more than 1-100th of an inch in thickness beneath the cornea, and are so arranged that all the rods stand at right angles to their respective facets. The layer of nerve cells behind the rods, is connected with the cephalic nerve centre by a number of very clear nerve filaments,—these are about 1-2500th of an inch in diameter. I shall call them collectively the optic nerves (Plate VII., figs. 1 and 5).

A thick chitinous ridge, probably the anterior margin of the dorsal plate of the fifth segment, surrounds the anterior edge of the compound cornea within, and bears an oval ring of chitine connected with it below by a narrow pedicle. This ring is very similar to the valves of the spiracles, and is jointed like them, both above and below. A thin loose membrane unites its outer edge with the edge of the cornea all round. A narrow tendon is connected with its posterior half about midway between its upper and lower joints; by means of which a small round muscle, which arises from the margin of the occipital foramen, is inserted into it; I shall call it the epineuron\* (Plate VIII., fig. 2).

A large tracheal sac, as has been already stated, spreads out behind the cephalic nerve centre, and almost surrounds the optic nerve. This sac sends a vast number of small tracheal vessels between the nerves and the epineuron, which dip into the spaces between the rods, forming a dense plexus around their inner extremities. A long slightly tortuous branch is given off from this

\* In giving this name I have been guided by its similarity to the epitrema, to which I believe it is homologous.

plexus, between each pair of rods, which runs directly towards the cones, tapering gradually to a fine blind point between them, but giving off no branches. These vessels are proportionally of large size, the diameter of the largest near its origin being quite 1-2000th of an inch. The use of these vessels is unknown; but the quantity of air supplied to them is manifestly controlled by the epineuron. They may be concerned in altering the shape of the cones and rods, so adapting the eye to distances or to changes of light; they certainly have a special function distinct from the supply of air to the structures of the eye.

The optic nerves connect the common retina with a layer of nerve cells, nearly 1-100th of an inch in thickness, which surrounds the outer portion of the optic or external ganglion —I shall call it the optic zone. This is largely supplied with long loops of tracheæ, which commence in a fine plexus between the zone and optic ganglion. The plexus is formed of vessels which dip in between the zone and ganglion, and give off very fine—almost straight—tracheæ, which form long narrow loops by again uniting on the surface of the optic zone, after having traversed its entire thickness.

The development of the compound eyes commences very early in the formation of the imago. When the pupa is removed from the pupa case on the fourth day, they appear as narrow transparent oval spaces externally. The optic ganglion, even at that early period, appears separated into two parts by a groove. The more external of these eventually forms the optic zone, and the rods and cones are represented by several layers of cells. On the fifth day, these parts are sketched out, as it were, in the cellular layers. Pigment appears on the sixth day of a faint rust colour, and all the parts of the eye are recognizable. The compound cornea consists at this period of a

#### THE OCELLI.

compact layer of cells, and the protodermic layer is distinctly divided into hexagonal facets.

Sometimes all these changes apparently take place a day earlier; but this is partly due to the change of colour in the larval skin taking place much earlier in some cases than in others. The imaginal discs are frequently unfolded to a considerable extent before the pupa case is formed. All the changes in the pupa are much affected by temperature, and I believe they are accelerated by heat.

#### Section XIII.—The Ocelli.

#### PLATE VIII., FIG. 8 & 9.

The Ocelli are three in number; they are situated in the frontal region, close to the bend in the occipito-frontal plate. The three corneæ have not their axes in the same direction; but are situated on the sides of a small eminence, so that their axes are divergent. Nevertheless they can all be seen from above, so that a simultaneous picture is probably formed on the three retinæ, in certain positions, although not upon corresponding portions in all the ocelli.

The corneæ of the ocelli vary in diameter, from 1-200th to 1-400th of an inch. They are smaller in the males than in the females, differing in this respect from the compound eyes. They are very convex, the inner curve being slightly greater than the outer, and their thickness varies, from 1-400th to 1-600th of an inch. In the adult insect the protoderm is not easily demonstrated over the ocelli, but from the manner in which they are developed, their structure is probably similar to that of the compound corneæ (Plate VII., fig 9).

I think it quite probable that, in both the compound and simple eyes of insects, the cornea consists of the protoderm and mesoderm; and the choroid or pigment layer of the modified endoderm. If so, they are essentially tegumentary organs, with the nervous structures piercing the endoderm, and expanding between it and the mesodermic layer.

Immediately behind the cornea are several layers of nerve cells; at least, I have not been able to distinguish any intermediate structure, although a fluid probably intervenes during life.

The nerve cells form a cone, about 1-600th of an inch in depth, from the back of the cornea to the entrance of the optic nerve. This is surrounded by a layer of hexagonal pigment cells, filled with bright rose-coloured pigment, and containing well marked nuclei. This choroid is surrounded by a plexus of tracheal vessels (Plate VII., fig. 8).

The ocelli first appear about the fourth day of the pupa state, and the pigment on their posterior surface is seen in beautiful hexagonal nucleated cells about two days later. During the whole pupa stage they are nearly twice as large as they are in the adult insect. In the same way, the legs and several other organs are larger when first formed, for condensation and contraction frequently accompany the development of organs in the pupa; but as the ocelli are flat at this period, something must be allowed to the subsequent convexity of the cornea.

#### THE ANTENNÆ.

#### Section XIV.—The Antennæ.

#### PLATE VIII., FIGS. 8 TO 13.

The antenna consists of six joints, of which the third forms the largest and most important part of the organ.

The first joint (Plate VII., fig. 9) is an irregular ring with four stiff setæ in front at its distal margin.

The second joint fits into the first and third. It consists of two parts. The posterior (upper) is sub-conical, notched in front, and covered with hairs, one of which on its outer side, is much longer than the rest. The membrane uniting it to the first joint is rough, with exceedingly minute hairs. The upper part of this piece fits into the cavity of the first joint which partially conceals it. The anterior (lower) portion is an inverted cone; its cavity opening posteriorly by a narrow ovate slit into the cavity of the third joint. The integument is reflected back from the margin of this slit to the base of the cone, and this reflection forms part of the wall of the third joint. The external surface of the cone, and that of the integument reflected back upon it, is covered with numerous minute crenated plicze, directed backwards, not more than 1-8000th of an inch in breadth, and 1-6000th of an inch in length—their use is unknown.

The third joint (Plate VIII., fig. 8) is elongated and ovate. Its surface is covered with minute hairs, between which are a vast number of pellucid dots, about 17,000 or 18,000 on each antenna, with about 80 large irregular spots, of a similar character, along the inner edge of the joint.\*

The smaller dots (Plate VIII., fig. 12) are about 1-5000th of an inch in diameter, or less. They consist of minute sacculi opening on the surface, by an extremely small pore, not more than 1-8000th or 1-10,000th of an inch in diameter.

\* First described by Dr. Braxton Hicks, Linn. soc. trans., Vol. 22. My calculations confirm their number according to the same author.

Dr. Braxton Hicks describes them as closed by a thin membrane, which he calls the outer layer of the antenna, evidently my protoderm. It appears to me however, from the most careful investigation, that the protoderm is reflected into them, but forms a thin perforated collar around the opening. The early period at which they appear in the pupa, seems to indicate that they are mere sacculi of the surface; the larger or compound sacculi are moreover, in all probability similar organs, and undoubtedly open upon the surface.

The larger spots (Plate VIII., figs. 11 and 12) are compound, consisting of several sacculi, with a common opening; the opening in these is often as large as 1-1500th of an inch. The several chambers are arranged in a radiating manner.

The fourth and fifth joints are mere rings, on the outer side of the third joint, near its proximal extremity; and the sixth forms a flattened plumose tapering bristle, which is solid through the greater part of its length in the mature insect.

The cavity of the first and second joints is chiefly occupied by cells, probably of endodermic origin; they are traversed by the antennal nerve.

The third joint is filled with pulp, which consists of cells and large nuclei, which are especially abundant, together with the terminal branches of the antennal nerve. This pulp is surrounded by a layer of very delicate brown pigment cells, which are immediately beneath the integument.

The antennal nerve splits up into numerous fibrillæ on entering this pulp, some of which terminate in ordinary nerve cells; but by far the greater number are covered with minute corpuscles, clustered round their terminations, like bunches of grapes (Plate VIII., fig. 13). A large tracheal vessel accompanies the nerve and ramifies in the pulp.

I believe the sacculi are minute expansions of surface, open freely to the atmosphere, and that the entire third joint is an olfactory organ. This seems probable, as the extensive ter-

# THE MAXILLARY PALPI.

minations of the nerve are brought into almost immediate contact with the air, being only separated by the extremely thin membrane of which the sacculi are composed; and likewise from the fact that the antennal nerves are given off from ganglia, next in magnitude and importance to the optic ganglia. Moreover, it appears more than probable that the olfactory sense or some modification of it is, if not the dominant sense, certainly only less important than vision to the insect. The third antennal joint is equally developed in both sexes; but the habits of the male are not sufficiently understood to justify any conclusions which might be drawn from this fact.

# Section XV. — The Maxillary Palpi. PLATE III. e., AND PLATE VIII., FIG. 15.

The minute structure of the maxillary palpi is so like that of the third joint of the antenna that its description naturally follows the description of that organ. The integument of the palpus is covered with short broad curved scales, about 1-2000th of an inch in length, as well as by the large hairs with which it bristles. Besides these there are a number of sacculi, about 1,000 on each palpus, each opening by a pore in the centre of a collarlike transparent ring, formed by the protoderm. Some of these sacculi are as large as 1-3000th of an inch in diameter, with an external opening about 1-5000th of an inch in diameter, but others are as small as those of the antennæ. They are very closely set about the extremity of the palpus, but are less numerous at its proximal end. The cavity of the palpus is filled with cells, chiefly belonging to the endoderm. A large nerve is distributed to it from the great nerve trunk

of the proboscis. Its filaments chiefly end in nerve cells in the extremity of the organ, where the sacculi are most numerons; a tracheal vessel accompanies the nerve in its distribution. It may be both an olfactory and gustatory organ, directing the insect to its food. However this may be, it can scarcely fail to be connected with the sense of taste, seeing that it is often enveloped in a drop of fluid regurgitated from the sucking stomach (see Section IV., page 55).

# Section XVI.—The Frontal Sac

#### PLATE I., AND PLATE VIII., FIG. 14.

The evidence that induces me to include this organ under those of special sense is, that its extensive surface, which is thrown into numerous plications, is still further increased by being covered with blunt papillæ (Plate VIII., fig. 14). Its internal surface is covered with yellow pigment, and with a thin layer of nerve cells connected with filaments from the antennal nerves. As has been already stated, its cavity is in free communication with the atmosphere, and the air contained must be frequently changed by the vibrations of the antennal plate.

With regard to the respective share which the antennæ, palpi, and frontal sac, probably have in the olfactory sense, we have little to guide us; but it appears to me likely, that the olfactory organs of the antennæ enable the insect to perceive odors, which are quite inappreciable to the vertebrata. If, as has been lately asserted, these are the organs which guide

#### THE CEPHALO-STEBNUM.

such insects as the male Kentish Glory moth to its female, which may be miles away, their power of appreciating odors would be little adapted for an insect when in the near vicinity of putrid carrion. The palpi, as has been already remarked, are probably gustatory organs, whilst I think it very probable that the frontal sac, the nerve supply of which is far more limited, and the structure of which is far coarser, is especially adapted for the appreciation of more powerful odors.

# Section XVII.—The Cephalo-Sternum.

# PLATE V., FIGS. 8-9, AND PLATE VIII., FIG. 16.

The relations and position of this organ have been sufficiently described.\* Its blades are covered with numerous sharp hairs or setæ. I can suggest no function which it is likely this remarkable organ subserves. Its blades are not more than 1-200th of an inch in diameter, so that it can hardly be concerned in the sound emitted by the insect when the head is rubbed against the thorax, nor does its position seem adapted to such a purpose. The only evidence that it is an organ of special sense is that its inner surface is covered with nerve cells.

\* Section VI., page 60.

# Section XVIII.—The Halteres and Wing Organs.

# PLATE VIII., FIGS. 3 TO 7.

The halteres are evidently modifications of the posterior wings. The halter consists of three portions: the base, which is covered with numerous special organs arranged in rows, the pedicle, and the globe.

The base is connected with the thoracic integument. Three hardened folds surround it, and have several slender muscles inserted into them. These move the whole organ, which is very movable.

The special organs at its base are arranged in four sets, two on the upper and two on the under surface. Each set consists of a series of curved ridges, under which these organs are placed. Three of the sets are represented in Plate VIII., fig. 3. The fourth is similar to the lower set, and is placed opposite to it.

The proximal sets form segments of a hemisphere, and the distal ones are arranged on two half-cylinders.

On making a section of the base, there appears to be but one cavity. If the two half-cylinders are completed internally, it is only by a thin membrane; but as each seems to open into the pedicle of the halter by a separate opening, I think this is extremely probable. The ridges under which the special organs are arranged are convex transversely, and each of the grooves between them bears a single row of curved hairs. These are close and long in the proximal sets, but short, strongly curved, and distant in the distal groups.

#### THE HALTERES AND WING ORGANS.

The organs themselves have been described as openings in the integument, closed by a thin convex membrane; but the appearance is deceptive, as far as I can tell, and I have examined these parts with great care. There are no openings in the integument, and the bright spots are entirely due to the presence of lenticular corpuscles of high refractive power beneath. By crushing the base of the halter in fluid between the thin glass and slide, I have succeeded in seeing these organs in profile, in situ (Plate VIII., fig. 6). I have been unable to discover their exact connection with the integument, but from the difficulty of displacing them, I suspect they are contained in sacculi. When set free, which may be effected by crushing the halter by a side motion of the thin glass, the bright spots disappear from the ridges, which could not happen if these were due to perforations; and the corpuscles appear free in the fluid. They are chiefly elongated, but a few are spherical. They vary in size from 1-3000th to 1-5000th of an inch in diameter. There are from 250 to 300 in each of the basal, and about 200 in each of the proximal sets, making nearly 1,000 in each halter.

The basal part of the halter becomes contracted, and forms the pedicle, which is connected with each of the two halfcylinders by a hollow ridge. The pedicle is clothed with fine hairs, especially at its distal extremity. It terminates in the globe, which is a hollow dilatation about 1-80th of an inch in diameter. The integument of the globe is extremely delicate and transparent. It exhibits rounded pigment spots of orange pigment beneath it, and has several large scattered hairs upon its surface.

The interior of the globe is occupied by a number of large vesicles about 1-300th of an inch in diameter, filled with and surrounded by fluid, which also fills the base and pedicle of the organ.

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The nerve of the halter, on entering the base, divides into several branches, the greater part of which end in nerve cells immediately below the corpuscles above described; but a large branch traverses the pedicle and ends in loops and nerve cells in the globe.

Before entering into any speculation as to the function of the halteres, I shall describe some closely allied structures, which I have named the wing organs. These are corpuscles exactly like those in the halter, arranged in rows and groups on the sub-costal nervure of the wing (Plate VIII., fig. 7). These corpuscles usually have a smoky tint, but I have no doubt as to their identity with the structures I have described in the halteres. They disappear in the same manner when the nervure is crushed. I have not, however, been fortunate enough to see them in profile. According to Dr. Braxton Hicks, they are very constant in insects in the same part, as well as on the sub-costal nervure of the posterior wings. They are supplied with nerve filaments, like the organs at the back of the halter.

These corpuscles, as well as those of the halteres, are opaque when they first appear in the pupa, and I have frequently observed those of the wing quite black and opaque in the perfect fly, as if their development had been arrested. Each of the wing organs seems to be situated under an oval convex portion of the sub-costal nervure, corresponding to the ridges of the halteres. Owing to their minute size, however, it is almost impossible to be certain whether these are convexities or depressions. There does not appear to be the slightest thinning of the integument at these points.

Looking only to the structure of these organs, I am inclined most strongly to regard them as auditory. The corpuscles are, I believe, otoconia. It is true, they are not acted upon by

# THE BALTERES AND WING ORGANS.

acetic acid, but the otolites of molluscs are not affected by prolonged treatment with it.\* I further think it extremely probable that the globe of the halter receives the undulations of sound, which are propagated through the fluid to these corpuscles.

Perhaps in insects not provided with halteres, the wings may receive the undulations of sound upon their whole surface, which are so propagated, probably less perfectly to the organs on the sub-costal nervure, which are very numerous in most genera.

With regard to the position of the organs, bearing in mind the rapid vibrations to which the integuments of the head and thorax are subject during flight, and more especially during the emission of sound, I conceive that the wings and legs aro probably the least agitated parts, and are hence fittest for the development of auditory organs. During flight, the expansion of the wing must evidently be the steadiest portion of the insect, as it forms the point d'appui upen which it moves. The halteres are certainly not much affected by the vibrations of the body; they are beautifully balanced by muscles, and are connected only by membranous integument with the flank.

To conclude this subject: we know the auditory organs of some saltorial Orthoptera are developed on their anterior, femora, and, according to Dr. B. Hicks, the wing organs are absent in the Orthoptera. Much careful work is needed however, in examining these structures in various genera.

The halteres are developed, like the wings, from a distinct imaginal disc.

\* W. Burnett's Translation of Siebold, Sec. 211, Note ii. H 2

#### Section XIX.—The Folliculate or Ductless Glands.

#### PLATE IX., FIGS. 2 AND 3.

The ductless glands are most abundant in the abdomen on the dorsal surface of the viscera, near the dorsal vessel, and

#### DESCRIPTION OF PLATE IX.

Fig. 1. The dorsal vessel.  $\times$  12 diam.

Fig. 2. A portion of one of the folliculate glands from the abdomen of a young fly,  $\times 25$  diam. 2 *a*, a portion of the same,  $\times 100$  diam. 2 *b*, a portion of the same, to show the ultimate distribution of the tracheæ and the cellular contents of the follicle,  $\times 500$  diam.

Fig. 3. A portion of one of the folliculate glands from the side of the dorsal vessel of the larva.  $\times$  40 diam.

Fig. 4. The epitreme of one of the abdominal spiracles.  $\times$  100 diam.

Fig. 5. The internal generative organs of the male.  $\times$  15 diam.

Fig. 6. The four posterior abdominal segments of the male, showing the loop and pouch in the position it occupies when the four segments are partially exserted. The dotted line indicates the position of this part when the segments are fully exserted.  $\times 10$  diam.

Fig. 7. A diagrammatic section of the last two segments of the abdomen in the male, in which a represents the penis, b the ventral plate of the penultimate segment, and c the dorsal portion of the last segment.  $\times$  10 diam.

Fig. 8. The last two segments of the abdomen of the male, with the ejaculatory organ and duct seen laterally.  $\times$  45 diam.

Fig. 9. The same seen from below.  $\times$  36 diam.

Fig. 10. The penis, with its palpi.  $\times$  60 diam.

Fig. 11. The apodé.ne of the penis, viewed from above.  $\times$  50 diam.

Fig. 12. The extremity of the penis.  $\times$  100 diam.

Fig. 13. The ejaculatory organ.  $\times$  100 diam.

Fig. 14. Spermatozoids. × 100 diam.





#### THE MALE GENERATIVE ORGANS.

also at the posterior extremity of the abdomen in the vicinity of the ovipositor in the female, and around the testes in the male. A small pair exist behind the optic nerves, and a second but still smaller pair may be observed adhering to the posterior cornua of the pharynx.

They consist of arborescent follicles (Plate IX., figs. 2, 2a, & 2b), which adhere to the tracheal trunks which supply them. The follicles are very transparent and structureless, but are largely supplied with minute tracheal vessels. In the young fly, they only contain nucleated cells, 1-3000th of an inch in diameter, free nuclei, and molecular matter; but later in the life of the insect they become loaded also with oil globules and granular cells, especially in the female, sometimes to such an extent that the abdomen becomes distended as if with mature ova; this fat disappears as the ova are developed.

A pair of folliculate glands\* (Plate IX., fig. 3) are found in the larva, one on either side of the dorsal vessel; each follicle contains one or two nuclei or nucleated cells. When the larva arrives at maturity they become filled with granular matter, and undergo disintegration before the formation of the pupa case.

# Section XX.-The Male Generative Organs.

#### PLATE IX.

'The male organs (Plate IX., fig. 5) are a pair of testes with their ducts, and a pair of albumen glands, which open with

\* Zellenstrangen, Weismann.

the ducts of the testes into a common duct—the vas deferens which terminates in an ejaculatory apparatus connected with the intromittent organ by a very narrow ejaculatory duct.

The testes are surrounded by a thick layer of folliculate glands, and are largely supplied with a plexus of nerves of organic life. Each testis consists of a sac of structureless membrane, lined with a bright reddish brown pigment membrane formed of coalesced pigment cells. In the earlier stages it contains cells in which the spermatozoa are developed, but is afterwards entirely filled with spermatozoa. The testis often presents an hour-glass contraction almost dividing it into two cavities. The length of the organ in its long diameter is about 1-30th of an inch. The duct of the testis is narrow, about 1-30th of an inch in length, and lined with conical epithelium.

The spermatozoa are very large, measuring 1-100th of an inch in length; their large extremity is a flattened disc 1-1000th of an inch in diameter, but the filiform appendage is exceedingly fine.

The albumen glands are sacs 1-15th of an inch in length; they are lined with cylindrical epithelium which secretes a very coagulable fluid; when the gland is mature its interior assumes a bright brown colour like that of the pigment coat of the testis, probably from an accumulation of pigment on the surface of its epithelial lining. The albumen glands open directly into the vas deferens by narrow necks.

The vas deferens is 1-10th of an inch in length; it is widest where it receives the ducts of the testes and albumen glands, being nearly 1-100th of an inch in diameter; at its outlet, it has only about half that calibre. It presents a very well defined

# THE MALE GENERATIVE ORGANS.

muscular coat of longitudinal and circular fibres, and is lined with cylinder epithelium.

The ejaculatory organ (Plate IX., 13) is a peculiar chitinous capsule, surrounded by a mass of muscles between the vas deferens and ejaculatory duct. It is about 1-100th of an inch in length in its longest diameter. It consists of a cup-shaped cavity,—the capsule,—from the smaller extremity of which a strong chitinous tube,—the manubrium,—projects. The manubrium terminates in a curved knob, which is perforated on its convex side by six or eight small apertures, and marked by two strong lateral ridges. These ridges are continuous with a membranous sac, which forms the inner extremity of the ejaculatory duct. The sac communicates with the interior of the knob by the perforations on its convex side.

The vas deferens perforates the manubrium near its junction with the capsule. The capsule is closed at its larger extremity, and numerous bands of muscle which surround the whole organ arise from the concave surface and edges of the knob-shaped end of the manubrium, and are inserted into the edges of the capsule close to its large extremity.

The ejaculatory duct is membranous, and not more than 1-1000th an inch in diameter; it is about 1-15th of an inch in length from its commencement at the ejaculatory organ to its termination at the end of the penis. The vas deferens, when examined immediately after it is removed, may be observed in a state of vigorous peristaltic action, by means of which the male fluid is, doubtless, conveyed to the ejaculatory organ. I have not been able to satisfy myself as to the existence of a muscular coat to the testes, but from the varieties of hour-glass contraction they exhibit, and the large supply of nerves which they receive from both senso-motor and sympathetic systems,

I cannot help suspecting their outer coat is contractile. The ejaculatory organ is evidently an elastic sac within a muscular covering, and aided by the peristaltic action of the vas deferens undoubtedly ejects the male fluid through the ejaculatory duct with considerable force, as the mass of muscles is very large indeed in proportion to the magnitude of the organ.

The four posterior abdominal segments (Plate IX., fig. 6 a. b. c. d.) form the external sexual apparatus of the male, and are included within the genital fissure, which is formed by the posterior margin of the fifth abdominal segment. This opening is almost entirely closed by four valve-like pieces (Plate IX., fig. 6 d), except during the sexual act, when the four segments are partially protruded from the fissure, and the valve-like pieces are directed backwards instead of forward.

The homologies of the several parts of these segments are very difficult to make out, and will require a lengthened study of the male and female organs of other insects before they can be determined with certainty.

There is no difficulty in recognising the dorsal plates of three segments, but the fourth seems to be represented only above, by the inner pair of valve-like pieces already mentioned. The ventral pieces are, however, considerably modified, and two appear to be fused together, quite an exceptional condition, for, as has already been remarked, the ventral are normally more distinct than the dorsal plates. Another anomaly is found in the unsymmetrical development of these plates, affording the only example of the want of perfect lateral symmetry in the integumental organs, and if the seminal receptacles of the female are excepted, in the structure of the insect.

The sixth abdominal segment presents only a very narrow thin dorsal

#### THE MALE GENERATIVE ORGANS.

plate which seems to coalesce laterally with the seventh, at least on the right side. The seventh and eighth are each very broad and strong, and are minutely tuberculated or shagreened on their surface. The eighth is deeply notched behind, the edges of the notch being produced laterally to form the external pair of valve-like pieces already mentioned. The internal pair of valve-like pieces are quite distinct from this plate, and surround the extremity of the rectum which opens between them ; they are united with the notch by a thin membrane. I believe they form part of the ninth segment.

The junction of the sixth and seventh segments on the right side is very considerably thickened, and supports, or more correctly these segments are supported, by a broad process which becomes gradually narrower, and curving round their ventral aspect forms a strong chitinous loop; a very rudimentary process exists on the left side, but never joins this loop. Numerous muscular bands are inserted into the edge of the loop, and a strong muscle is attached to its thick extremity. The loop forms a hinge upon which the four posterior segments move. It is united loosely by membrane to the ventral plate of the fifth and to the ventral plate of the eighth segment. The membrane between it and the eighth segment forms a pouch, which contains the male organ when the segments are retracted; the loop then lies along the inner margin of the notch in the fifth abdominal ventral plate (Plate IX., fig 6 represents the position of the loop both during the exsertion and retraction of the four posterior segments).

The eighth segment is continuous with the outer valve-like appendages (Plate IX., figs. 8 & 9), which are curved and covered upon their outer surface with hairs directed forwards; they probably embrace the ovipositor during copulation.\* Externally each is prolonged forward as a slender but strong-curved rod, which unites it with a heart-shaped ventral plate. The rods lie along the lateral margins of the genital fissure (Plate IX., fig. 9), and the ventral plate with which they are united, lies within its anterior border; it is united by the membranous pouch with the loop.

The posterior prolongations of the dorsal plate are probably not to be

\* I have never been able to observe the sexual act in the blow-fly. When kept in captivity I have never known them either to perfect ova or spermatozoa, neither have I been able to hear of anyone having observed the act. By comparing the organs carefully, I have attained the results which I have set down as the probable relations and uses of the various parts concerned.

regarded as the dorsal lateral appendages, as they are continuous with the plate itself as well as with the lateral rods. But the ventral plate of this segment is deeply notched on either side behind, and a pair of curved hollow nipple-like organs, each bearing several setæ, are articulated with these notches; they evidently represent the inferior lateral appendages and probably curve over the leaf-like organs on the dorsal aspect of the ovipositor. The dorsal prolongations of this segment act as springs; when at rest they are directed forward, and lie with their broad surface in a horizontal position; when the segments are partially protruded, they are turned back with their broad edges directed vertically; this is effected by muscular action through the medium of the lateral rods.

The remainder of the sexual apparatus consists of a single segment. The internal valve-like pieces which surround the rectum are probably its dorsal lateral appendages; this will appear more likely by comparing them with their homologues in the female which are separated by a small triangular dorsal plate. (Plate X., fig. 5.)

The intromittent organ (Plate IX., fig. 10) probably represents the ventral lateral appendages of the same segment, fused more or less into one. It presents perfect lateral symmetry, and is supported by a hinge-joint upon a very large apodéme (Plate IX., fig. 11); each lateral half is articulated separately with this apodéme, and each bears at its base a palpus-like organ articulated with it by a distinct ginglymus joint. The two lateral halves are united by a curved spine or crest, which arches over the ejaculatory duct.

Each lateral half consists of a slightly curved hard rod of chitine, broad at its base, but gradually becoming thin towards its extremity, which is terminated by a small triangular knob. About half way between the base and apex of each of these rods on its under side is a projecting process which bears a curved plate, serrated along its inferior border, and uniting with its fellow in the mesial line. These plates terminate in pointed processes at their outer posterior angle, but their middle portion is continued backward, and turns up to surround the ejaculatory duct, which lies upon the upper surface of these plates except at their posterior extremity, where they form a complete tube, united anteriorly with the duct, and opening posteriorly in a broad trumpet-shaped mouth. (Plate IX., fig. 12.)

The intromittent organ is moved by a mass of muscles arising from the handle-like apodéme which supports it; these are inserted into the lateral halves of the organ as well as into the bases of its palpus-like appendages; other muscles arise from the eighth ventral plate, and are inserted into the apodéme.

Unless the apodéme represents the ventral plate of the ninth segment,

which I strongly suspect it does, this is only represented by its four lateral appendages.

The intromittent organ is 1-30th of an inch in length, which corresponds with the distance between the external opening and the neck of the bursa in the female.

The relations of the crest and palpus-like appendages during the sexual act, are, probably, as follows :--The crest is brought into relation with the interior of the last joint of the ovipositor, distending the extremity of the oviduct, whilst the palpus-like organs are in relation with its lateral surfaces externally.

The palpus-like organs are apparently sensory. They are hollow, slightly curved, and terminated by thin rounded spoon-shaped blades the concave or posterior border is furnished with a single row of stiff hairs. The base presents a well-marked articular surface formed of two parts at right angles with each other.

Section XXI.—The Female Generative Organs.

PLATE X., FIGS. 1-7.

The female generative organs (Plate X., fig. 1) consist of the ovaries and their ducts, the common oviduct, the bursa, the seminal receptacles, the albumen glands, and the ovipositor. The ovaries are circular discoid masses of ova, situated at the sides of the abdomen, and largely supplied with tracheal vessels from the second abdominal spiracles. They consist of numerous follicles which terminate the oviducts, each follicle containing a series of ova, one behind the other, in various stages of development. The follicles are so arranged that the ova are packed side by side with their long diameters vertical to the surfaces of the disc of the ovary. The oviduct commences upon the inner surface of the disc by the union of the follicles, and the outer surface

#### DESCRIPTION OF PLATE X.

Fig. 1. The internal generative organs of the female seen from below only a portion of the ovaries is represented, from a preparation stained with carmine.  $\times$  15 diam.

Fig. 2. The common oviduct and its appendages, viewed laterally, to to show its muscles and bursa.  $\times$  30 diam.

Fig. 3. The ovipositor seen laterally, during the deposition of an egg.  $\times$  30 diam.

Fig. 4. Plate between the rectum and ovipositor.  $\times$  30 diam.

Fig. 5. The last segment of the ovipositor.  $\times$  30 diam.

Fig. 6. The bursa copulatrix.  $\times$  40 diam.

Fig 7. The seminal receptacles of the female from the right side  $\times$  60 diam.

Fig. 8. One of the ovarian tubes or follicles exhibiting four ova in various stages of development—a the germinal vesicle surrounded by epithelium-like cells; b the first stage of yolk segmentation; c the second stage of yolk segmentation. d the segmented yolk broken up and surrounded by a zona pellucida.  $\times$  60 diam.

Fig. 9. Yolk cells undergoing degeneration. a—mature yolk cell, b c & d the same undergoing degeneration.  $\times$  250 diam.

Fig. 10. Upper part of an ovum, showing the first stage of the formation of the germinal disc and yolk canal.  $\times$  60 diam.

Fig. 11. The ovum just before impregnation.  $\times$  60 diam.

Fig. 12. The upper extremity of the same, showing the micropyle, germinal disc, and upper part of the yolk canal.  $\times$  150 diam.

Fig. 13. The ovum, eight hours after impregnation, showing the larval integment in the interior.  $\times$  60 diam.

Fig. 13a. Cells from the larval integment of the same age.  $\times$  500 diam.

Fig. 14. The ovum, twenty-four hours after impregnation, showing the tracheal system of the larva just before its escape from the egg.  $\times$  60 diam.

Fig. 15. A small portion of the ovicapsule at the time of impregnation.  $\times$  200 diam.

Fig. 16. Cells from the fat bodies of the adult larva.  $\times$  30 diam. *a*, the same in the first stage of degeneration. *b*, *c*, growth-corpuscle formed from the same, and nucleated cells originating in the growth-corpuscles, The former  $\times$  30, the latter  $\times$  300 diam.

Plate X





#### THE FEMALE GENERATIVE ORGANS.

is covered by a dense mesh of tracheal vessels. When the insect first emerges from the pupa, the ovaries are not 1-30th of an inch in diameter, but when the ova are mature they occupy the greater part of the abdominal cavity; for the mature ova are 1-20th of an inch in length, and on the most moderate computation, each ovary contains 300 mature ova, so that a single female is capable of producing at least 2,400 ova, supposing the four sets in the ovary to be matured in succession.

The ovarian follicles appear to consist of structureless membrane, largely supplied with delicate tracheal vessels, and the oviducts in the young insect consist entirely of an exceedingly fine membrane. When mature, they exhibit a thick muscular coat of transverse and longitudinal fibres. They unite with each other at the base of the ovipositor, and are continued to its extremity as a common oviduct.

About 1-20th of an inch from the extremity of the ovipositor, the albumen glands and seminal receptacles open into the common oviduct.

The albumen glands are simple sacculate glands, 1-15th of an inch in length, which open into the oviduct by narrow necks. They secrete a viscid fluid, which covers the ova after impregnation, rendering them opaque. It is quite insoluble in water, but is immediately dissolved by æther, rendering the ova again transparent.

The seminal receptacles (Plate X., fig. 7) are three in number, two upon the right and one upon the left side. Each consists of an ovate dark brown chitinous capsule, measuring about 1-120th of an inch in its long diameter, connected with the oviduct by an elastic tube, 1-20th of an inch in length, continuous with the wall of the capsule.

The capsule exhibits well marked rings of chitine and numerous nuclei. It is easily ruptured by pressure. The elastic tube connecting the capsule with the oviduct has a very thick wall, of a light yellow tint, marked with transverse wrinkles. The calibre of the tube is greatest in the middle, where its diameter does not exceed 1-400th of an inch. It tapers gradually to a very fine opening at either extremity. Numerous small cells may be observed adhering to the duct, which give it a beaded appearance. They are probably concerned in the development of the muscular coat which surrounds both the capsule and its duct, but which is not well developed until the ova are mature.

A little below the openings of the albumen glands and seminal receptacles, about 1-30th of an inch from the outlet of the common oviduct, its membranous coat forms a pouch in its ventral wall. This pouch is called the bursa copulatrix (Plate X., figs. 1, 2, and 6). It is about 1-80th of an inch in diameter. The bursa has a narrow neck, which opens backwards into the oviduct. It exhibits two curious lateral folds, one on each side of the neck, which project into its interior, as if the wall had been pushed inwards, and a third fold in the mesial line, which forms a partial septum, dividing the pouch into two lateral halves. The bursa is very elastic, resuming its shape after dilatation or compression, and refracts light powerfully. The neck of the bursa is studded with minute corpuscular bodies, with a bright transparent centre. These are not more than 1-5000th of an inch in diameter, and may be either papillæ, connected with nerves, or merely centres of chitinous deposit. I am decidedly inclined to the latter view.

The arrangement of the muscular fibres of the outer coat of the oviduct below the entrance of the ducts of the albumen glands and seminal receptacles, needs special notice. The muscular coat is very highly developed (Plate X, fig. 2), and its outer layers form broad bands of muscle, chiefly having an oblique direction round the oviduct. A well marked broad band surrounds both the bursa and oviduct in a transverse direction, and conceals other layers which have an oblique direction; and others again, which surround only the bursa or oviduct separately. A pair of large muscles, which arise from the dorsal part of the second segment of the ovipositor—the seventh ab-

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dominal segment—are inserted into the oviduct before and above the bursa, and a second pair from the same part of the eighth abdominal segment are inserted into the oviduct between the bursa and its outlet. The internal or membranous coat of the oviduct is continuous with the integament at the extremity of the ovipositor.

The function of the bursa is clearly to receive the male fluid, but a few hours after copulation all the spermatic filaments disappear from both the bursa and the oviduct. They are then found in a dense mass, closely coiled together in the capsules of the seminal receptacles. Nothing, then, remains in the bursa but the two masses of coagulated albumen, one of which occupies each lateral half. These gradually disappear, either by deliquesence or absorption. The manner in which the spermatic filaments are transferred from the bursa to the receptacles is unknown, but the transference is probably effected by their own movements. Upon one occasion I found the upper part of the oviducts of a fly, which had been immersed in spirit for four-and-twenty hours, filled with spermatic filaments, which were still in a state of active movement. I suppose the insect had been captured immediately after copulation, and that the spirit had not permeated the oviducts. owing to the coagulation of the albumen around them, so that the filaments, no longer directed into the ducts of the spermatic receptacles by the contraction of the oviduct above their openings, found their way into the upper part of the oviducts.\*

The external organ in the female consists of a lengthened ovipositor, which is retracted when at rest within the posterior

<sup>\*</sup> In Burnett's Translation of Siebold, p. 450, note v., the spermatic filaments are stated to be conveyed from the bursa of insects to the receptacles by their own movements, which agrees perfectly with the result of my researches.

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opening of the fifth abdominal segment. It consists of four segments, the anterior three of which are separated by membranous interspaces equal in length to the segments, and when the organ is retracted each segment is withdrawn within the next anterior to it, like the draw-tube of a telescope. The posterior segment is attached closely to the penultimate, and, like the ninth abdominal segment in the male, is considerably modified, and bears a pair of leaf-like appendages which terminate the rectum.

The first and second segments of the ovipositor are like the abdominal segments; they consist of a dorsal and ventral plate, and have a fringe of long vibrissæ-like setæ along their posterior margin. The third consists of three plates, two of which are dorsal or lateral, and the third is ventral; it is slightly cleft posteriorly, and its extremity is covered with hairs.

The fourth segment (Plate X., fig. 6) consists of a small triangular dorsal plate which bears a pair of leaf-like lateral appendages covered with hairs. These surround the dorsal part of the opening of the rectum. The intestine is separated from the oviduct by a curved semicircular plate (Plate X., fig. 4), the angles of which are anterior and prolonged as apodémes which give insertion to a pair of muscles, which arise from the ventral plate of the third segment, and embrace the oviduct. Its curved border is posterior and is fringed with hairs. It is probably the ventral plate of the last abdominal segment; if such is the case, the oviduct opens between the last and penultimate segments of the ovipositor on its ventral aspect.

The development of the sexual organs commences in the larva, and so presents an exception to the other organs of the imago. The ovaries or testes are found as a pair of cellular bodies adhering together on the under side of the rectum, near its termination. Dr. Weismann\* figures both male and female organs in this condition, and asserts that even at that early period they present distinctive characters. I have been unable to verify this assertion, although I believe it is likely that Dr. Weismann is quite correct in this, as in most of his elaborate researches.

\* Kolliker's Zeitschrift. Band XIV.

THE DEVELOPMENT OF THE OVUM.

#### Section XXII.—The Development of the Ovum.

# PLATE X., FIGS. 8 TO 14.

The ovum in the earliest stage of development in which I have yet succeeded in observing it, is ovate in form, and measures about 1-300th of an inch in its long diameter. It consists of a single cell,—the germinal vesicle,—which occupies the greater part of its interior, and is surrounded by a thin layer of clear fluid. This is covered by an external envelope of minute cells—the yolk sac—1-3000th of an inch in diameter, loosely adherent to each other, and contained in an extremely delicate membrane—the ovi-capsule. These cells refract light strongly, and make it very difficult to observe the germinal vesicle.

The ovum soon after becomes globular; the external cells adhere firmly to each other, and become prismatic by pressure; and the yolk, instead of containing a single vesicle, consists of six to eight cells, which fill the whole interior of the yolk sac. I am doubtful whether this multiplication of cells is analogous to yolk-segmentation in vertebrates, but I suspect that it is.

The ovum now enlarges rapidly, assumes an ovate form, and the yolk cells become spheroidal, multiplying until about thirty-two are contained within the ovum (Plate X., fig. 8 c), after which they degenerate into a homogeneous molecular mass. A clear space is then gradually formed at the upper part of the yolk, which is the representative of the germinal disc in vertebrates.

The changes which take place in the yolk cells are very remarkable: at first they exhibit a cell wall and a large nucleus, but after a time the

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contents of the cell form a well-marked mass around the nucleus separated from the cell wall by a clear space (Plate X., fig. 9 a). Sometimes one or more small shining nuclei appear in the clear space, and the central mass becomes nebulous, and degenerates into molecular granules. Occasionally it becomes segmented into two or four, previously to its degeneration (Plate X., fig. 9, b, c, d). Ultimately the cell wall disappears, and the whole yolk becomes homogeneous (Plate X., fig. 8 d, represents the yolk during the degeneration of its segmented cells).

The ovum has by this time attained its full size. The ovicapsule becomes separated from the cellular layer or yolk sac beneath, by a clear area corresponding to the zona pellucida, and the wedge-shaped cells of the external layer of the yolk, the yolk sac, become converted into hexagonal chitinous cells of pavement epithelium. (Plate X., fig 15).

The ovicapsule forms a bladder-like projection at this period at the upper extremity of the ovum, immediately above the germinal disc, and a groove commencing at the germinal disc is gradually formed between the yolk sac and the yolk. (Plate X., fig. 10). The germinal disc and the groove or yolk canal may now be observed to be surrounded by rapidly growing cells; and a group of cells appears at the upper extremity of the germinal disc. This may be distinctly seen to surround a minute canal—the micropyle—by means of which the germinal disc communicates perhaps directly with the inflated portion of the ovicapsule. These changes take place before impregnation.

The groove or yolk canal is the only part within the yoke sac which remains unaltered after impregnation, and it may be observed, even after the larva has escaped from the ovum, as a distinct line on the interior of the yolk sac.

The length of time required for the development of the ovum up to this point is unknown; for, although I have

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repeatedly kept flies for the purpose of discovering it, I have never succeeded in getting the ova developed in captivity, perhaps from the want of a proper kind of food. However well fed, the insects only laid by large stores of fat in the ductless glands.

Impregnation is usually effected immediately before the eggs are laid, the spermatozoa being probably discharged from the spermatic receptacles upon the upper extremity of the ovum, and brought into immediate contact with the whole length of the yolk through the medium of the micropyle and yolk canal. Immediately after the discharge of sperm, or simultaneously with it, a viscid fluid is poured upon the ovum probably from the albumen glands, which renders it glossy and opaque. The act must be rapidly performed, for although the ova are usually extraded from the evipositor in quick succession, none escape impregnation.

Soon after impregnation, a layer of rapidly-growing cells appears in the place of the germinal disc, and along the inner surface of the yolk canal; this layer forms the ventral portion of the integument of the larva. At the end of eight hours it has extended so as to surround the entire yolk. The whole integument is then sketched out by this cellular layer, and its segments are divided by well-marked folds.

At this period, or soon after, the alimentary canal appears sketched out by a cellular membrane—the inner or mucous layer of the cells which surround the yolk. At first it is straight and very capacious, including the whole yolk, but it becomes gradually narrow and tortuous during the formation of intermediate layers of cells, from which the other internal organs are developed. When the larva is hatched, it still contains the remains of the yolk.

Beyond these facts, I can add little with any degree of certainty, except that twenty-four hours after impregnation, the newly developed tracheal vessels of the embryo become suddenly filled with air, and the larva commences to struggle in the egg, but soon ruptures the ovisac and escapes.

Dr. Weismann has traced the development of the embryo larva far more minutely than I have, in his "Entwicklung Der Dipteren;" but I confess I do not know how he has attained such well-defined results from the very delicate cellular structures of the embryo, nor do his figures appear to me so accurate as those of the imaginal discs, and the development of the pupa.

# Section XXIII.—The Formation of the Pupa.

#### PLATE VI., FIGS. 1 TO 4.

The nature of the changes which take place during the formation of the pupa have been already briefly indicated. They closely resemble those in the Echinodermata, where the perfect form is developed in the interior of the larva. But the change is even more remarkable in the fly, as all the tissues of the larva undergo degeneration, and the imaginal tissues are re-developed from cells which originate from the disintegrated parts of the larva, under conditions similar to those appertaining to the formation of the embryonic tissues from the yolk.

The formation of the pupa may be conveniently studied under two heads—the formation of the pupa skin, and the transformation of the larval tissues.

The pupa skin is partly formed from seven pairs of delicate

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cellular expansions, called by Dr. Weismann imaginal discs, and partly from cells formed upon the inner surface of the larval integument. When mature, it is an extremely delicate, apparently structureless transparent membrane, presenting no trace of its cellular origin, and, after the escape of the imago, remains as a fine silvery membrane in the interior of the pupa case.

The imaginal discs have received the following names from Dr. Weismann, which I have retained, and simply translated into English, the antennal and optic discs\* which enter into the formation of the head, and the inferior pro-thoracic and meso-thoracic discs  $\dagger$  which are chiefly concerned in forming the anterior and intermediate limbs.—These are all attached firmly through the medium of short nerve trunks to the nerve centres of the larva. (Plate VI., fig. 1)

The superior meso-thoracic disc, ‡ and the superior and inferior metathoracic || discs are firmly attached to the lateral tracheal vessel near the anterior spiracle. The superior discs are chiefly concerned in forming the wings and halteres, and the inferior in the formation of the posterior limbs. (Plate VI., fig. 2). Beside these a horse-shoe shaped arch of similar tissue is attached to a pair of tracheal vessels, in front of the supracesophageal ganglia, and above the antennal discs. It is called the ring by Dr. Weismann, but I believe it is the upper pro-thoracic disc.

The abdominal portions of the pupa skin are formed from cells developed upon the inner surface of the corresponding larval segments.

Each imaginal disc is enclosed in a capsule of structureless membrane. The capsules of those attached to the nerve centres appear to consist of the neurilemma of the nerves which support them, but the capsules of those attached to the traches seem to be derived from the outer coat of the tracheal vessels. The discs are formed of minute cells, having a granular appear-

- \* Autennen and Augensheiben.
- + Unter prothoral scheibe, and meso-thoral sheibe.
- t Ober meso-thoral sheibe.
- || Ober and unter meta-thoral sheiben.
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ance. The rapid development of the discs ruptures the capsules which contain them; but during their development, before the rupture of the capsule, they present the appearance of spiral folds and concentric rings—the optic and superior thoracic discs having the former, and the inferior thoracic discs having the latter kind of folds.—The antennal discs present the appearance of concentric rings at their anterior extremity.

The unfolding of the concentric ring-like folds is exceedingly curious, the internal ring being pushed out first, the rest following in succession. These form the joints of the limbs and antennæ.

The development and unfolding of the inferior thoracic discs is represented in Plate VI., figs. 1, 3, and 4. At first the several discs are separated entirely from each other, but as they are developed and enlarged, the discs belonging to each pair become closely united by the common origin of their capsules (fig. 3). The concentric rings each form a tarsal joint, and other rings which are developed later, form the tibia, femur, and coxa. After the rupture of the capsule, the disc presents the appearance represented in fig. 4.

The superior thoracic discs, after rupturing their capsules, form sacs, in the interior of which the wings and halteres are developed.

The pupa covering of the thorax is probably formed entirely from these discs; but according to my observations the inferior meso- and metathoracic discs take no part in the formation of the proper thoracic walls. These seem to be formed entirely from the inferior pro-thoracic and superior meso- aud meta-thoracic discs. If such is the case, my views concerning the number of thoracic segments would acquire confirmation. The pro-thorax being formed from the pro-thoracic discs; the anterior spiracle, which opens between the pro-thorax and meso-thorax, would belong to the next thoracic segment, undeveloped in the imago, but forming the sixth segment in the larva, and bearing, its anterior spiracles, whilst the superior meso- and meta-thoracic may belong to segments which alternate with the inferior thoracic discs.

The antennal and optic discs form the pupa covering of the head, and the optic discs present a strongly-marked spiral fold before the rupture of their capsules.

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The semi-fluid cellular matter, from which the imago is developed, is derived partly from the disintegrated tissues of the larva, and partly from the fat bodies or omenta.

After the larva ceases to feed, if the temperature be sufficiently high, the tissues begin to degenerate. The muscles may be observed at this time in a state of continuous activity, rythmic contractions commencing at one extremity of each set of fibres, and passing regularly with a wave-like motion to the opposite extremity. At the same time, large bright nuclei, 1-1000th of an inch in diameter, appear in rows in the centre of the muscular fibres. These are ultimately set free by the degeneration and waste of the muscles, and exhibit a granular appearance, but are readily distinguished by their great transparency and low refractive power.

At the same time a series of remarkable changes take place in the fat bodies, which consist in the adult feeding larva of flattened hexagonal cells filled with very opaque, highly refractive white granular matter. These cells now begin to exhibit clear spaces in their centre, which presently become converted into nuclei exactly like those formed in the muscles. The granular matter of the omental cell then becomes condensed about the nucleus, leaving a clear space around the circumference of the cell; the cells separate from each other, and the cell wall undergoes disintegration.

The free nuclei developed from the muscular fibres of the larva now begin to collect around them aggregations of molecular matter, derived from the degeneration of the muscles and other larval tissues, so that all the nuclei are soon surrounded by similar molecular aggregations, each about 1-150th of an inch in diameter.

The precise nature of the changes which take place imme-

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diately afterwards are more difficult to observe, but after the second day of the pupa state, numerous delicate nebulouslooking cells, about 1-1000th of an inch in diameter, replace some of these aggregations, and bright nuclei, 1-3000th to 1-5000th of an inch in diameter, make their appearance amongst them. The majority of the aggregations remain, however, and become more dense toward their circumference. The growth of the imaginal tissues evidently proceeds at the expense of some of these aggregations, whilst those which remain, undergo marked changes; they increase in size, lose their original nuclei, and become invested by a delicate membrane. When the imago emerges from the pupa, a large number of these corpuscular aggregations remain in all parts of the insect; they disappear during the development of the imago. and when it is mature, not one can be detected. I propose the term growth-corpuscles to designate these remarkable bodies.

The growth-corpuscles of the imago, when it emerges from the pupa, vary from 1-80th to 1-200th of an inch in diameter. They contain molecules and granules of various sizes, besides numerous nucleated cells, 1-1000th of an inch in diameter, with a well-defined cell wall, and from one to three large nuclei. The exact manner in which these corpuscles are concerned in the development of the tissues is, at present, unknown ; their functions may be similar to those of the folliculate glands,—the preparation of the nutritive fluid or formative plasma. I do not think they are directly converted into tissue either in the pupa or imago.

All these changes are much influenced by temperature, and the entire development of both the mature larva and the pupa in all its stages is immediately stopped when the temperature falls below 45° Fahrenheit. This circumstance alone preserves the species through the winter, all the larvæ and pupæ existing being entirely checked in their development, undergo hybernation. Their dormant vitality remains, however, to be awakened by the warmth of spring.

When the imago is ready to burst from the pupa case, the anterior extremity is forced off by the dilatation of the frontal sac. This is effected by the contraction of all the muscles then existing, which forces the greater part of the circulating fluid into the frontal sac, and distends it until it far exceeds the head in size. At this period a pair of large muscles extend from the edges of the frontal sac to the margin of the occipital foramen. They assist in the dilatation of the sac by diminishing the cavity of the head by their contraction. They afterwards undergo degeneration, and may be looked for in vain in the mature insect.

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